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Selection of Traits for Growth, Form, and Wood Quality in a Population of Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) from British Columbia

by

© JOHN N. KING

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF FOREST SCIENCE

EDMONTON, ALBERTA
SPRING 1986

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Selection of Traits for Growth, Form, and Wood Quality in a Population of Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) from British Columbia submitted by JOHN N. KING in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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Date 14 March 1986

Abstract

Selection of traits for growth, form, and wood quality were investigated in full-sib progeny trials of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) in British Columbia. Sources of variation for additive genetic variance were significant for 20 of 21 traits investigated. Other sources of genetic variation (dominance genetic variance and G.E.I. sources of variance) were, by and large, non-significant. High individual tree heritabilities were found for branch angle ($h_i^2=0.73$) and wood density ($h_i^2=0.90$), indicating that these traits would respond well to mass selection. Traits of form including branch number, partitioning traits (branch to stem diameter ratios and branch length to total height ratios), stem sinuosity, early height measurements, and diameters showed moderate heritabilities ($h_i^2\geq0.15$; $h_f^2\geq0.7$). Other form traits: forking and bole taper; and growth traits of later height measurements, stem volume, and direct branch growth measures were of low individual tree heritabilities ($h_i^2\simeq0.10$; $h_f^2\simeq0.50$). However all traits except for branch thickness (non-significant) indicated that they would respond well to family selection. Expected response to stem volume selections are large ($\simeq$10% per selection intensity unit) because of large phenotypic variance among family means. Moderate and favourable genetic correlations exist between traits of yield, and traits of crown form, and partitioning. Unfavourable genetic correlations exist

between traits of yield and wood density (r_A=-.53) and between traits of form and wood density. These parameter estimates are similar to results published both for Douglas-fir and other conifers.

Genetic parameters were used to establish key traits that can be effectively measured and used in Douglas-fir progeny evaluations. They were also used to point out important strategies that can be used in genetic selections. Early height can be effective for early selections for traits of growth and yield. Later selections for growth and yield are more efficiently made with diameter measurements. Partitioning traits are more effective for form selections than direct crown measurements. Genetic covariances among crown form traits and yield traits can be effectively exploited to promote a fine-branching form type. Several selection index options were investigated to deal with the strong negative correlation that exists between wood density and diameter growth. Selections that maximize the minimum expected response to both traits would offer the best strategy and would help to break down this negative correlation.

Options for incorporating these selection strategies into current breeding practices are briefly discussed.

Acknowledgments

There are many people I wish to thank for their help and interest in this study. A lot of credit must go to Chris Heaman and his predecessor Dr. Orr-Ewing who initiated this experiment and whose material I have been allowed to work with; Chris imparted a lot of his enthusiasm to this project. I would like to thank my supervisor Dr Francis Yeh for his involvement and the commitment from a busy schedule that he gave to this study. I wish to thank Ingemar Karlsson and the staff at the Cowichan Lake Forest Experimental Station for their help and hospitality. I would like to thank Dr Bruce Dancik for his editorial comments and criticisms, and Dr John Worrall for his comments on my manuscript. I wish to acknowledge the excellent financial support provided by the C.F.S. through the Department of Forest Science and N.S.E.R.C. for providing personal support. I finally wish to thank my wife Patty for all her help and support without which I could not have completed this study.

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1. INTRODUCTION

1.1 Biology and Thesis Objectives

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) dominates the most productive forest lands of western North America (Silen 1978). It is valued in this region and in areas where it has been introduced as an exotic (Birot 1982) for its growth potential, good form characteristics, relative freedom from major pests, and superior wood quality. It is, therefore, a candidate for tree improvement programs in the many parts of the world where it is planted. The purpose of this thesis is to investigate the potential for genetic improvement for traits of growth, form, and wood quality in a population of coastal Douglas-fir from Vancouver Island and the southern mainland of British Columbia.

1.1.1 Systematics and Distribution of Douglas-fir

Eight species of the genus *Pseudotsuga* are recognized, two in western North America and the others in Asia (Isaac and Dimock 1965). The genus *Pseudotsuga* is distinguished by its woody cones with persistent scales and protruding trident-like bracts; by conical, sharp-pointed buds; by linear, soft leaves; and by resin blisters on smooth bark that becomes furrowed and marbled with cork layers as it matures (Hosie 1973; Silen 1978). One of the species of the genus found in North America is big-cone Douglas-fir

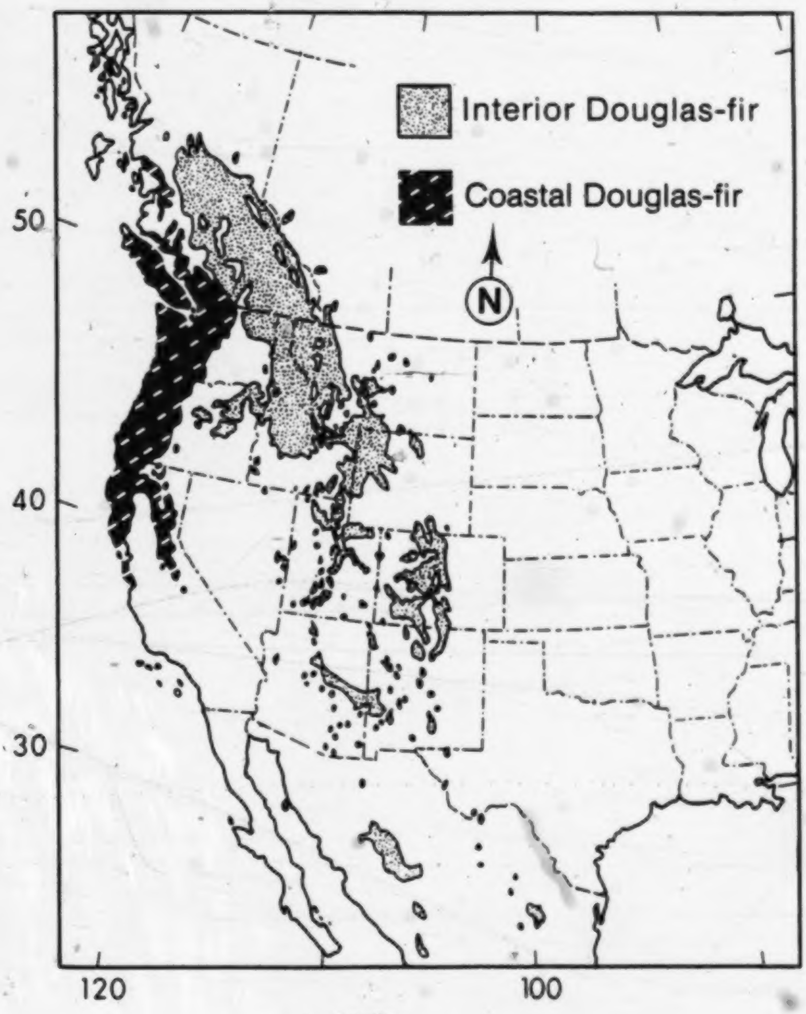
(*Pseudotsuga macrocarpa* Mayr), which has a limited range in California (Griffin and Critchfield 1972). The other species (*Pseudotsuga menziesii*) is a wide-ranging gymnosperm occurring from central British Columbia (lat. 55° N.), south along the Pacific Coast to Central California (lat. 37° N.), inland to western Alberta and down the Cordilleran chain to southern Mexico (lat. 19° N.) (Fig. 1). Elevational distribution varies with latitude ranging from over 800 m in the extreme northern part of its range, to over 3350 m for some Rocky Mountain sites (Silen 1978). Within its range rainfall varies from 450 mm to over 5000 mm per year.

The wide and varied environments together with the isolation potential of mountain topography have produced a species of extreme genetic diversity. Two main varieties are recognized: coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) and interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco). The coastal variety is the more commercially valuable of the two and was the first-recognized form of the species. References in this text to Douglas-fir refer primarily to the coastal variety unless otherwise stated.

1.1.2 Ecology and Silvics of Douglas-fir

Over its wide range Douglas-fir prefers moist, well drained soils; although intolerant of wet soils and anaerobic conditions, it can be relatively tolerant of summer droughts. In the cold, wet conditions of the coastal

Figure 1. Natural range of Douglas-fir, *Pseudotsuga menziesii* (after Little 1971).


Interior Douglas-fir
Coastal Douglas-fir
N
50
40
30
120
100

fog belt other conifers such as Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) are favoured. On poorly drained soils and on floodplains, Sitka spruce, western redcedar (*Thuja plicata* Donn.), and hardwood species such as cottonwood (*Populus trichocarpa* Torr. & Gray) are better able to survive (Krajina *et al.* 1982). The coastal variety does not tolerate frosts below -10°C for a period of more than about a week (Krajina *et al.* 1982). At high elevations it is replaced by cold-hardy species such as mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), western white pine (*Pinus monticola* Dougl.), and lodgepole pine (*Pinus contorta* Dougl.).

There are difficulties on many good sites with the establishment of Douglas-fir due to competition from shrubs (Silen 1978, Klinka *et al.* 1981). This is a particular problem on more moist soils, where it is more shade intolerant (Krajina *et al.* 1982) and shrub growth is vigourous. Compared with its commonly associated conifers, Douglas-fir ranks as a shade intolerant species (Isaac and Dimock 1965). Because of its association with shade tolerant species such as western hemlock, Sitka spruce, western redcedar, grand fir (*Abies grandis* (Dougl.) Lindl.), and amabalis fir (*Abies amabalis* (Dougl.) Forbes), Douglas-fir is recognized as a sub-climax species (Isaac and Dimock 1965). However, over much of the Pacific slopes, a region associated with summer droughts, Douglas-fir occurs in essentially pure, even-aged stands as the major conifer species. Douglas-fir's thick fire-resistant bark, rapid growth and long life span make it a highly successsful fire climax species. The noted longevity of Douglas-fir (more than 1000 years) (McArdle *et al*. 1961), and its ecological relationship with fires (Schmidt 1960) has established its dominance in the forest community.

The nutritional requirements of Douglas-fir are moderate, but it grows poorly on oligotrophic soils, where calcium, magnesium, nitrogen, phosphorus and potassium are in low supply (Krajina *et al*. 1982).

1.1.3 Breeding Methods and Goals

The growth potential and high quality timber of Douglas-fir have made it the prime species for intensive forestry practices and tree breeding in the Pacific Northwest. British Columbia's tree improvement program for Douglas-fir began in 1957 with phenotypic selection of plus-trees (Orr-Ewing 1969). Selections were made for growth and form from a broadly defined seed zone of coastal British Columbia and Northern Washington (Heaman 1967). First generation orchards currently provide much of the seed for the reforestation program (Yeh *et al*. 1981).

The breeding program in B.C. has developed: i) to establish a breed population for recurrent selections, ii) to estimate genetic variances and establish parameters as an aid to selection, and iii) to test the breeding values of first generation selected parent trees (base population). The vehicle for this program is a disconnected six-parent half-diallel genetic test of the base population (Heaman 1981). An earlier factorial test (Yeh and Heaman 1982; EP707) of 26 trees chosen randomly from the base population is limited in its opportunity of allowing recurrent selections but provides excellent research material for objectives ii) and iii). This factorial test offers the ideal material for research because:

1. it is full-sib material from a factorial mating design, thus it permits the direct estimation of additive and dominance genetic variances (Namkoong 1979);
2. it is at an age where traits of form and quality traits can start to be evaluated;
3. it allows the opportunity of researching selection strategies that can be applied in the larger-scale breeding program.

Traits of quality refer to traits that affect the quality of the clear-wood resource. Specifically these are traits of crown form, stem form and wood quality. Traits of crown form are: branch angle, branch number, branch thickness, and branch length. Crown form traits are important, not only for their effect on the clear-wood resource - heavier and more persistent branches (knots), more compression wood, less strength in stress grading of lumber and poorer pulp and paper yield and quality; but also for management and handling - pruning and delimbing costs, and also because of their importance to the partitioning for valuable bole wood rather than undesirable branching material. Branch thickness and branch length can also be considered as growth traits. Traits of stem form refer to straightness of stem, stem taper, and forking, and are important for their effect on the quality and uniformity of the clear-wood resource. Wood density is considered the most important clear-wood characteristic affecting wood quality for pulp, lumber, and plywood (Kellogg 1982).

1.1.4 Objectives

This thesis attempts to address the question of whether it is possible to select for traits of growth, form, and wood quality in Douglas-fir, using parameters estimated from a genetic experiment (EP707) established by the British Columbia Ministry of Forests, Research Branch. The specific objectives are:

1. to test for the significance of genetic sources of variation and estimate genetic parameters for traits of growth, form and wood quality;
2. to establish key traits of growth, form and wood quality that can be effectively measured and used in large-scale progeny test evaluations;
3. to investigate multiple trait selection strategies for the genetic improvement of Douglas-fir.

1.2 Growth of Douglas-fir

Height and growth are not only prime economic traits, but in a species such as Douglas-fir, which forms pure even-aged stands following fire (Schmidt 1960), height is an important component of fitness. Suppression and eventual mortality will occur for genotypes that cannot remain in competition with their neighbours within the dominant and co-dominant canopy classes.

Initial seedling growth (prior to six years) can be slow (Isaac and Dimock 1965) for Douglas-fir, but this probably reflects environmental constraints (Silen 1978). Once past the seedling stage annual growth can surpass 2 metres, and 60 cm annual height increments can continue for a century on best sites (Silen 1978). Volumes of over 1500 m^3/ha are not unusual in stands of coastal Douglas-fir (Silen 1978).

1.2.1 Variability Studies on the Growth of Douglas-fir

Douglas-fir achieves its greatest growth potential in Oregon and Washington west of the Cascades, southern coastal British Columbia, and Vancouver Island. In these regions, its stature and height (often exceeding 70 m) give it an imposing presence in old growth stands.

On the west coast of North America there is, in general, a cline of growth rate potential that follows a westward trend of increasing precipitation and availability of moisture in summer drought times (Silen 1978). Variation attributable to environmental clines associated with elevation or soil moisture gradients can occur even in small-scale geographic distributions (Silen 1978, Campbell 1979).

The exploitation of seed source differences can be profitable in tree improvement programs and is a necessary first step in species introductions (Birot 1982). White and Ching (1985) found that once the poor southern Oregon provenance was removed, the differences among 13 other provenances - using 25 year field performance - was slight and often not statistically significant. One of the earliest provenance variation studies was the Douglas-fir Heredity Study (Munger and Morris 1936) established in 1912. The study was based on 120 open-pollinated (O.P.) families from 13 sources in western Oregon and Washington and was planted on five sites. Namkoong *et al.* (1972) used this study to look at time-trend results in genetic and environmental variances. Although in the end they felt they could only make general inferences from one site, they found a steady and significant increase between seed-source means as the test matured after age 15. Jarret (1978) found an increasing provenance effect with age in the French IUFRO[1] provenance trials.

Provenance research for coastal Douglas-fir in B.C. has revealed that large and real differences among seed sources can be exploited, especially by the introduction of

---

[1] International Union of Forestry Research Organizations

Washington provenances into mild coastal sites (Illingworth 1978, Ying 1984). Introduction of low-elevation provenance material at high elevation sites (above 900 m) involves the risk of severe snow or frost damage (Ying 1984). If gains from seed-source selections are to be realized, care must be taken that these gains are not lost to reduced hardiness and adaptability (Silen 1978).

The capture of a racial effect through wide crosses has also been investigated in Douglas-fir and may offer some promise (Orr-Ewing and Yeh 1978).

1.2.2 Genetic Variation in the Growth of Douglas-fir

Variation within populations is maintained as a method of temporal adaption for a long living species such as Douglas-fir (Hesslop-Harrison 1964). Several published accounts report that significant and important amounts of additive genetic variance are available for improvement of growth traits in Douglas-fir. Campbell (1972) found significant differences but low heritabilities (h_i^2[2] =0.10-0.16) for height increments of full-sib seedlings. Yeh and Heaman (1982) reported significant values for sources of additive genetic variance (σ_f^2) for height and diameter at age six in the same material used in this study. Heritability values were, h_i^2=0.14±0.10 and 0.19±0.11 for height and diameter respectively. Estimates of non-additive genetic variances were non-significant. Genetic studies of Douglas-fir in France show moderate heritabilities and expected response to selection. Jarret (1978) found, using height at eight years on 15 open-pollinated families within one of the IUFRO provenances, moderate heritability values (h_i^2=0.36±0.19). Birot and Christophe (1983) reported heritability estimates from 26 provenances of the French Douglas-fir trials that ranged from 0.0 to 0.77 for height at 12 years. Most of the provenances had levels of $h_i^2 \approx 0.3$; and heritabilities of tree girth were similar. Fashler *et al.* (1985) also reported significant amounts of additive genetic variances and moderate to high within-provenance heritabilities for height growth from O.P. seedlings from IUFRO collections at the U.B.C. Research Forest. Rehfeldt (1983) found high within-population heritabilities for height growth in four-year-old O.P. seedlings of interior Douglas-fir (h_i^2=0.52±0.10).

---

[2] h_i^2=heritability appropriate for mass (phenotypic) selection, Appendix Table B

In comparison with these O.P. studies the full-sib studies of Campbell (1972) and Yeh and Heaman (1982) have reported significantly lower heritabilities. Heritability estimates derived from open-pollinated families are biased when the assumption is made that the genetic covariance between O.P. progeny is that of half-sibs (Namkoong 1966; Squillace 1974). Although Rehfeldt (1983) adjusted for an inbreeding coefficient of F=0.10 this bias may account somewhat for the differences between the O.P. studies and the full-sib studies. The testing environment and age of material are also important factors in the determination of environmentaly sensitive traits such as height growth. Nursery and farm field trials show higher heritabilities than progeny trials that simulate production plantations and heritabilities for height growth can decline with age.

Namkoong *et al.* (1972) found later height measurents in the Douglas-fir Heredity Study (Munger and Morris 1936) were non-significant ($P > .05$) for family differences.

1.3 Form of Douglas-fir

Mature Douglas-fir is characterized by a long, branch-free, cylindrical stem and a short, columnar, flat-topped crown (Hosie 1973). Young trees have narrow conical crowns that extend to the ground (Hosie 1973). In a closed stand lower limbs die rapidly with increasing overhead shade. However natural pruning of these limbs can take some time (Isaac and Dimock 1965). Branching and crown-form traits are important for the effect they have on the quality of the clear-wood resource; compression wood is increased with acute angled branching, and heavy limbedness will produce persistent knots and retard the ability to produce clear stems (von Wedel *et al.* 1968). Clear stem wood is not only desirable for clear-wood products and peeler logs (von Wedel *et al.* 1968; Shelbourne 1970), but also in the production of uniform pulp products (Blair *et al.* 1974; Zobel and Kellison 1978).

Crown characteristics are likely to be important not only because of their effect on wood quality, but also because the biomass potential of the species is more valuable when partitioned into stem wood than into undesirable branch wood.

1.3.1 Variability Studies on the Form of Douglas-fir

Extreme phenotypic variability for limb and crown characters was found by Campbell (1958,1961,1963). Campbell measured crown characteristics (branch numbers, lengths, thicknesses and angles) in 15- to 35-year-old Douglas-fir using 30 trees in each of 10 locations. Most of the variability of these characters could be accounted for by the variability in volume, except for that of branch angle. Relationships between branch number and volume, branch length and volume, and branch thickness and volume were strong and positive. Age of the tree had little influence, except for its influence on volume. Campbell found the following relationships between branch characters:

1. trees with acute-angled branches have thicker branches,
2. trees with fewer branches have thicker and longer branches,
3. taller trees of similar volume (less tapering) have shorter branches.

However, the association between branch characteristics was slight in comparison to the association of branch characters with volume.

Campbell (1963) used path-coefficient analysis to look at the branching relationships with volume. Stem volume was most affected by variation in the number and thickness of branches. Most of the effect branch length had on volume was indirect through branch thickness. Branch number and branch thickness together were associated with 60% of the variation in stem volume. These relationships were fairly consistently expressed in the eight separate areas studied, at least when grown in open-growth conditions.

Because environmental influences such as spacing, nutrients, and site quality exert a strong influence on form characters, significant differences for these characters between populations could not be verified as indicating genetic differences (Campbell 1961). Campbell also found that the phenotypic variation of branching characters was most highly expressed in areas of good height growth. Site factors exert a strong influence on the expression of form characters, and studies of their effect in Douglas-fir have been made by Walters and Soos (1961), De Champs (1978), Carter *et al.* (1985).

Jarret (1978) found a strong and significant replication effect for crown-form traits in the French IUFRO provenance-progeny trials. He also found that provenance effects were significant for crown-form traits: branch angle, branch number, knot index[3], and distribution of branches in the whorl, but not for branch thickness. A significant negative phenotypic correlation ($r=-0.58$) existed between the elevation of a provenance and its branch number. Sources from lower elevations had more branches than high elevation sources. Jarret also found that northern provenances tended to have more acute-angled branching than southern provenances.

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[3] knot index was a ratio of cross-sectional areas of branches to the cross-sectional area of the stem 10 cm below the whorl (Campbell 1961).

1.3.2 Genetic Variation in Crown-Form Characteristics

Heritability estimates for crown-form traits vary, but tend to be larger than those of growth traits. Heritability estimates (h_i^2, appropriate for mass selection) for branching-quality traits in Finnish trials of Scots pine (*Pinus silvestris* L.) were 0.4 - 0.7, whereas growth traits were low to moderate (< 0.3) and sometimes lower than 0.1 (Poykko 1982). Merrill and Mohn (1985) found non-significant family differences in Lake States white spruce (*Picea glauca* (Moench) Voss) for total height and branch number; but significant heritabilities (h_i^2) of 0.14 for diameter, 0.16 for branch thickness, and 0.44 for branch angle.

The inheritance of branch quality traits in Douglas-fir shows similar trends (Jarret 1978; Birot and Christophe 1983). A comprehensive study of crown-form traits was conducted by Jarret (1978) using 15 O.P. families within one of the provenance's of the French IUFRO provenance. Heritabilities were reported as:

Trait	h_i^2
Branch number	non-significant
Branch angle	0.54±0.23
Branch thickness	0.34±0.18
Knot index	0.29±0.16

Non-significant results for branch numbers per whorl are similar to those reported for white spruce (Merrill and Mohn 1985) and may reflect the difficulty in assessing this trait (Campbell 1961).

Branch angle, in other studies on the French provenance-progeny material (Birot and Christophe 1983), showed a strong additive genetic effect similar to that reported by Jarret (1978). Twelve percent of the variation could be attributed to differences between families within provenances, whereas only 1.5% of the variation was attributed to provenances. Heritabilities were high ($h_i^2=0.49$), and large phenotypic variabilities indicated response to selection for this trait would be good (Birot and Christophe 1983). Jarret (1978) found moderate additive genetic variance for branch thickness, which contrasted to the non-significant effect he found for this trait for provenances.

1.3.3 Stem Form Traits

Although Douglas-fir stands appear relatively straight-stemmed and of good form, a surprising amount of sweep and sinuosity can occur. In stands marked for commercial pilings, where only slight deviations from straightness are permissible, seldom could 20 per cent of the trees be used (Silen 1978). Stem crookedness can increase the amount of undesirable compression wood reducing pulp yield and quality (Zobel 1971) and producing poorer quality lumber and plywood (Shelbourne 1969a). Orr-Ewing (1967) in a limited study of stem form showed that selection might be useful for stem straightness.

Sinuosity, stem crookedness confined within an interwhorl stem segment (Campbell 1965) (Fig. 2), is a conspicuous feature of young Douglas-fir. There is typically a reduction of sinuosity from the pith to the bark in young trees (Polge and Perrin 1984), and much of the minor crookedness that occurs at this stage is covered by eccentric wood growth as the tree matures. However, this dislocation from the vertical brings about the formation of compression wood (Burns 1920; Mergen 1958). A portion of compression wood may be left adjacent to the pith in what otherwise would be considered a straight tree; the amount of which may be directly related to the degree of sinuosity (Zobel and Haught 1962). In severe cases a permanent wave may be left in the stem.

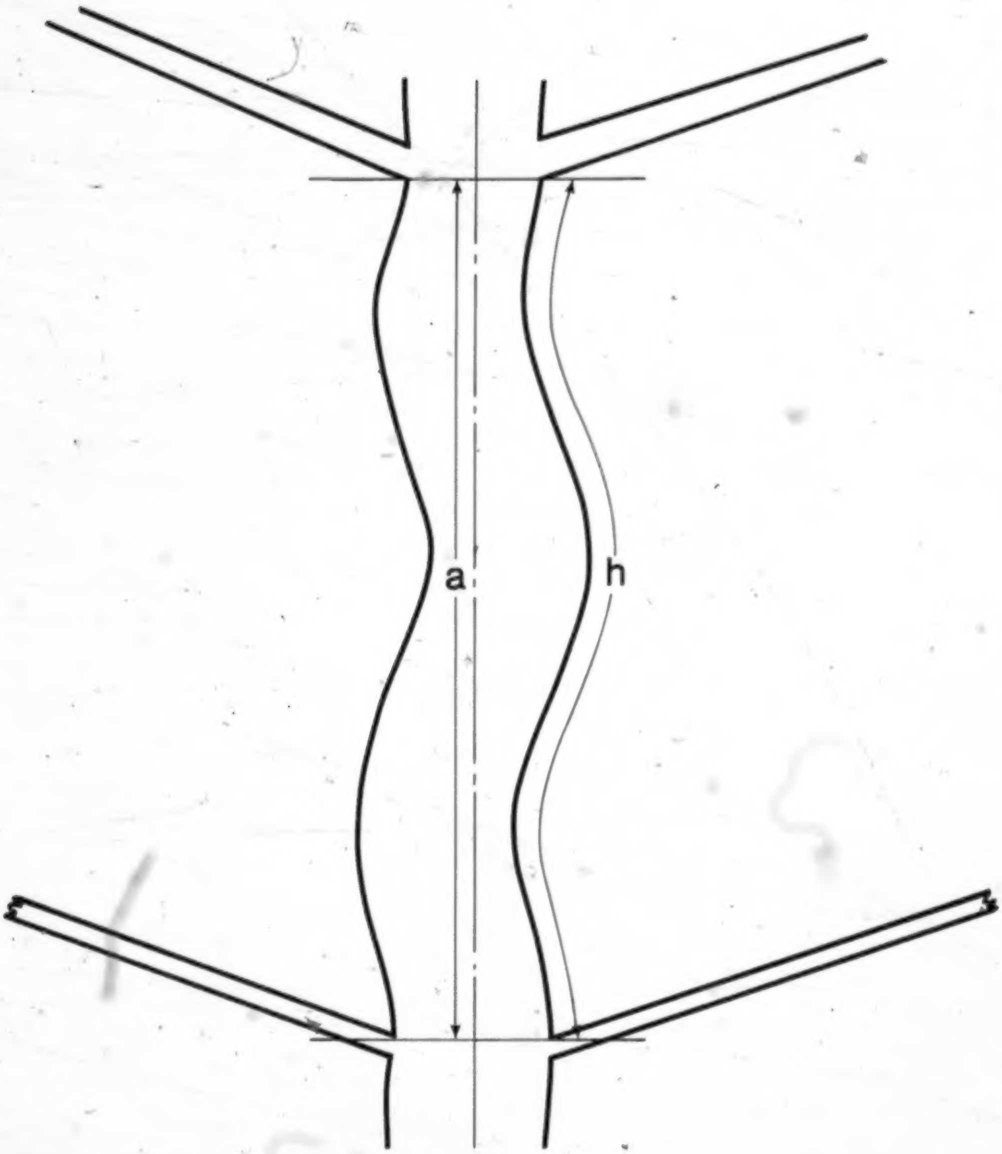

Figure 2. Sinuosity in Douglas-fir (Campbell (1965) measured sinuosity using a transformation of the ratio of *h/a*, where *a* equals the vertical length of the interwhorl and *h* equals the length along the sinuous stem).

Campbell (1965) studied sinuosity in Douglas-fir stands. He found high within-population variation (CV=42%) and significant between-stand variation for stem sinuosity. Using path analysis he showed diameter at the base of a leader was better associated with sinuosity than was length of leader. Although not working with genetic material, Campbell predicted that heritability was likely low; thus sinuosity would be a difficult character to improve through mass selection.

Forking, ramicorn branching[4], and multiple leaders are other commonly occurring features of young Douglas-fir. The incidence of these growth features in young Douglas-fir is strongly associated with the occurrence of lammas shoots.

Lammas shoots or second, late-season flush is a common feature of the phenology of young Douglas-fir (Fig. 3). Lammas growth is defined as an abnormal burst of late-season shoot growth from the flushing of recently formed buds that are not expected to open until the following year (Kramer and Kozlowski 1979). Lammas shoots occur with high incidence in young plantations of Douglas-fir (Walters and Soos 1961) and are associated with favourable climatic conditions, good site quality, fertilization (Walters and Kozak 1967) and origin of provenance (Jarret 1978). However, they decline with age and are relatively uncommon in material over 12 years of age. These types of late-season shoot growth, are

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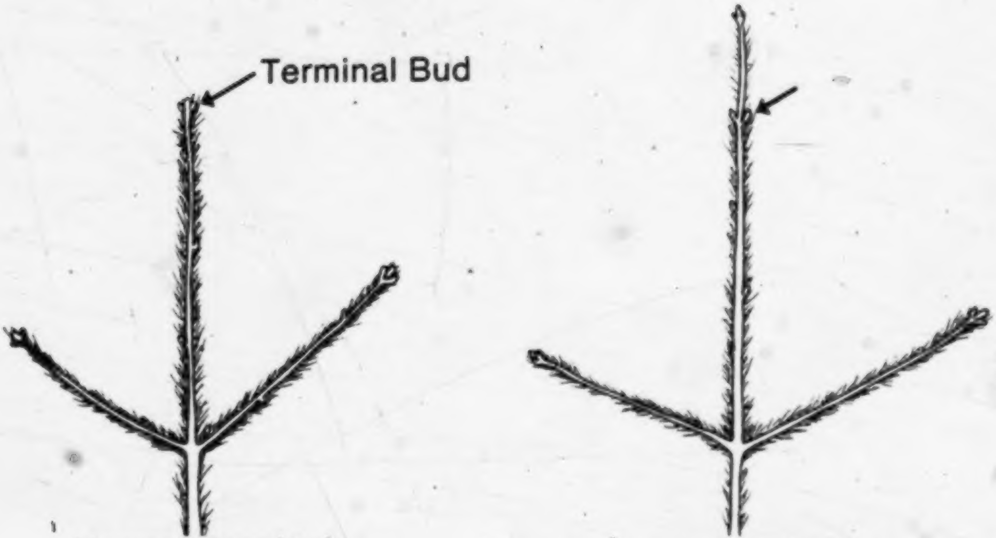
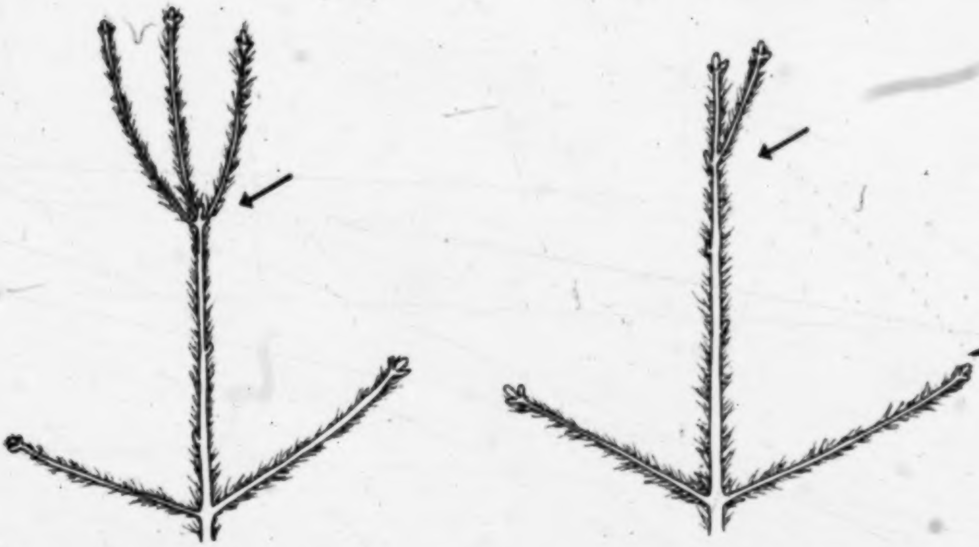
[4] a ramicorn branch refers to a fastigiate, large, thick branch that is associated with lammas shoots from lateral buds (Fig. 3)



Normal Terminal Shoot Growth

Lammas Shoot From Terminal Bud



Lammas Shoots From Lateral Buds

Lammas Shoots From Terminal and Lateral Buds

Figure 3. Abnormal late-season (lammas) shoot growth.

one of the most important juvenile growth features that promote distorted growth symptoms (Carter *et al.* 1985). They are most often manifested in young Douglas-fir plantations as multiple lateral-bud lammas shoots or a combination of lammas shoots from the terminal and lateral buds (Fig. 3); the common consequences are forking, ramicorn branches, multiple leader formation, and excessive branchiness and clusters of branches (Rudolph 1964). Growth disturbances associated with secondary flushing are exasperated when early frosts occur. Although such growth deformities at a juvenile stage may be overcome, they can leave permanent detractions from a clear bole.

Stem taper is a valuable trait for its effect on yield and quality. Trees with marked taper have greater volume than trees of the same height where taper is less evident. A cylindrical stem is more profitably handled and processed for dimensional timber. Much of stem taper depends upon spacing and other silvicultural practices; genetic influences on stem taper are little understood. Jarret (1978) found a slight provenance effect for stem taper.

1.3.4 Genetic Variation of Stem Form Features

Jarret (1978) studied sinuosity and forking and found:

Trait	h_i^2
Sinuosity	0.52±0.23
Forking	non-significant

Response to selection for sinuosity was high, due to the high heritability and large phenotypic standard deviation. Moderate to, high family heritabilities of sinuosity (h_f^2 >0.5) and large variation among families indicated that selection for stem straightness would be favourable in studies by the Pacific Northwest Tree Improvement Cooperative (Adams and Howe 1985). Sinuosity was reported to be of moderate heritability (h_i^2=0.39) in the study of Birot and Christophe (1983); as with Jarret (1978) forking and ramicorn branching were found to be non-significant. Birot and Christophe (1983) noted that sinuosity as well as the crown-form traits are sensitive to non-controlled environmental effect (85% residual variation), but because of large phenotypic variances among families, family selection can be very effective.

1.4 Wood Quality in Douglas-fir

The timber of Douglas-fir is highly prized and sought for structural uses, pulp and veneer. It is straight grained, moderately light to moderately heavy (wood density of 430 to 450 kg/m^3) and of intermediate durability (Cown 1976).

Wood density is not a single property, but is a complex of characteristics such as percentage of summerwood, cell-wall thickness, cell diameter, lignin content, etc. (Koch 1972); however, it is convenient to treat it as a single trait. Wood density is an important trait because of its close relationship to the strength, quality, and yield characteristics of pulp products (Barefoot *et al*. 1970), and the strength and structural properties of clear-wood products (Barrett and Kellogg 1984). In a fast-growing plantation it is important to maintain the density found in the indigenous resource (Zobel and Kellison 1978) and breed for a uniform product (Zobel *et al*. 1982).

1.4.1 Variability Studies of Wood Density of Douglas-fir

Single-tree estimates of wood density are complicated by substantial vertical within-tree variation, but much of this variation is predictable (Cown 1976), and wood density estimates from breast high increment cores can give a good indication (r=0.91) of weighted tree mean density (Cown 1976). Another consideration is the use of young trees to evaluate mature tree performance. Do early progeny evaluations of wood density offer reasonable guidelines for later, mature-tree wood density? Wood density increases with age and there are indications that this increase is linear and can be quite predictable. Northcott *et al*. (1964) in a study of variation patterns in a limited number (six) of Douglas-fir trees demonstrated this trend after an initial period of instability prior to the 10th year growth ring. Kellogg (pers. comm.) in a recent study of Douglas-fir demonstrated a similar trend, with under 6-years being highly unpredictable 8- to 12-year growth rings stabilizing, and after 12-15 years demonstrating an increasing linear trend. Keller and Thoby (1977) showed significant phenotypic correlations between mean density of the first ten rings to mean density of the outer ten rings in two stands of 30- and 60-year-old Douglas-fir, but non-significant correlations for another smaller population of 60-year-old Douglas-fir. Although McKimmy (1966), working on the Douglas-fir Heredity Study (Munger and Morris 1936), recommended that predictions of stem densities not be made before 25 years, McKimmy and Campbell (1982) suggested tests on 10- to 15-year-old material could provide information applicable to older material. Other studies by Harris (1965), Thoby (1975), Keller and Thoby (1977), Reck and Sziklai (1973) and especially Cown (1976), have demonstrated that early wood material can be used to predict mature stem-wood density in Douglas-fir. These studies have indicated that wood deposited after 15 years can be acceptable for whole-tree wood-density comparisons, but wood in the 8 to 12 year range can offer, with some caution, the earliest possible evaluation of whole-tree wood density.

Although several studies have shown differences among regions and provenances (Drow 1957; USDA 1965; McKimmy 1966; Wilcox 1974; Thoby 1975) this variation is by and large minor in relation to variation among individual trees (Cown 1976, Cown and Parker 1979).

1.4.2 Genetic Variation in Wood Density

Heritability values - appropriate for mass selection - were high (h_i^2 most provenances > 0.8) for wood mean density from 14-year-old provenance-progeny trials in France (Bastien *et al.* 1985); genetic variability was much higher at the family level than the provenance level, confirming a similar observation made by McKimmy and Campbell (1982). Bastien *et al.* (1985) reported that potential gain for wood density would not be great because of the low phenotypic standard deviation; they also reported unfavourable correlations between wood mean density and growth traits and wood mean density and wood heterogeneity. Unfavourable genetic correlations between growth and wood density, and between form and wood density have also been reported in radiata pine (*Pinus radiata* D.Don) (Dean *et al.* 1983).

The Pilodyn wood tester has been used to assess wood density by using the wood's resistance to penetration by a spring-loaded pin (Cown 1978). Moderate-to-strong negative correlations of depth of pin penetration with wood density from a variety of conifers suggest that this may be a useful way of ranking families for wood density selections:

$r = -0.86$	radiata pine	(Cown 1978)
$r = -0.81$	loblolly pine	(Taylor 1981)
$r = -0.71$	silver fir[1]	(Hoffmeyer 1978)
$r = -0.83$	white spruce	(Micko *et al.* 1982).

Many of these studies are on larger, more mature trees, where the bark has been removed, and may be less applicable on through-the-bark measures of juvenile-growth trees.

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[1] *Abies alba*

In order to assess this instrument for its use in making genetic selections, genetic correlations are more appropriate to look at than phenotypic correlations.

Sprague *et al.* (1983) found high genetic correlations and resulting efficiencies of indirect selection for two types of Pilodyn:

$r_A = -0.89$ 2.0 mm needle, 6joules spring,

$r_A = -0.82$ 3.0 mm needle, 18joules spring,

but disappointing results for a third type ($r_A = -0.24$; 2.5 mm 18j). Bastien *et al.* (1985) concluded that the Pilodyn was not effective for selection purposes in the French Douglas-fir provenance-progeny tests. Genetic correlations were inconsistent and too greatly influenced by environmental factors, although they suggested that the Pilodyn might be used for quick measurements not requiring great accuracy.

2~~.~~ MATERIALS AND METHODS

2.1 Materials

Twenty-six trees were randomly sampled from the base population of first generation selected parent trees of coastal British Columbia. (Table 1, Fig. 3). Twenty-two trees (serving as seed parents) were crossed with four trees (serving as pollen parents) in April 1971 (mating design II "tester", Comstock and Robinson 1952). Seeds from all families were spot seeded in nursery beds and at the end of the first growing season, in the fall of 1972, the seedlings were transplanted into Styro 8 plugs containing a mixture of peat, sand and sterilized soil. In the spring of 1973 one group of seedlings was outplanted in the Greater Victoria Watershed (GVWS); in the following spring another group was outplanted at the Cowichan Lake Experimental Station (CLES). Progeny families were planted in a randomized complete block design with three replications of nine-tree plots at a spacing of 3 m × 3 m. Both sites were cleared and fenced prior to planting.

1. Cowichan Lake Experimental Station (elev. 165 m) was planted with 9-tree row plots. CLES is on an undulating topography. Soils are Humo-Feric Podzols and are coarse sandy loams in texture. Soil moisture regime ranges from dry to moist and soil nutrient regime from poor to rich. Rooting depth is greater than 100 cm (Klinka *et al.* 1984). Survival has been high at this site.

2. Greater Victoria Watershed (elev. 488 m) was planted with 9-tree square plots. GVWS is on a uniform slope gradient of 20-25% and a SSE exposure. It is on a Coarse Loamy Podzol with a soil moisture regime of dry to fresh and a soil nutrient regime of medium with a rooting depth of over 100 cm (Courtin 1983, Klinka *et al.* 1984). The site is presently unfenced and has had problems with browsing, first by grouse and rabbits, and later by deer. Both Armillaria root rot (*Armillaria mellea*) and laminated root rot (*Phellinus weirii*) are present. Problems have also occurred due to severe competition with broom (*Cytisus scoparius*), which mainly affects the lowest replication where there are deeper and more mesic soils. Because of the damage and lower survival at this site, the full set of measurements could be made on less than half the trees.

Measurements of height and diameter have been made at both sites at 6 years (Yeh and Heaman 1982), 10, and 12 years. Growth form measures were taken at 11 years (summer 1983), and wood density measures (taken only at CLES) were taken after the 11th growing season (winter 1984).

TABLE 1. Parent tree locations.

Tree no.†	Location	Elevation	Lat.	Long.
Seed Parents				
49	Parksville	685 m	49°17'	123°33'
57	Gold R.	150	49 52	126 06
60	Campbell R.	30	50 15	125 24
72	Koksilah	550	48 37	123 48
73	Cowichan	180	48 50	124 10
110	Powell River	290	49 52	124 19
193	Chilliwack	625	49 07	121 36
300	Howe Sound	370	49 36	123 19
303	Howe Sound	610	49 36	123 19
305	Victoria	90	48 27	122 34
310	Pitt River	300	49 42	122 43
314	Pitt River	425	49 42	122 43
315	Pitt River	225	49 42	122 42
323	Pitt River	370	49 41	122 43
408	Chilliwack	825	49 07	121 49
415	Skagit	510	49 03	121 05
418	Knight Inlet	400	51 05	125 35
422	Sechelt	435	49 26	123 52
439	West Vancouver	615	49 22	123 13
499	Kelsey Bay	150	50 26	126 14
549	Knight Inlet	150	50 50	125 50
623	Powell River	335	49 52	124 19
Pollen Parents				
28	Ladysmith	685	48 56	123 53
33	Cowichan	580	48 50	124 05
62	Sproat Lake	60	49 18	125 13
448	Garibaldi	625	49 51	123 08

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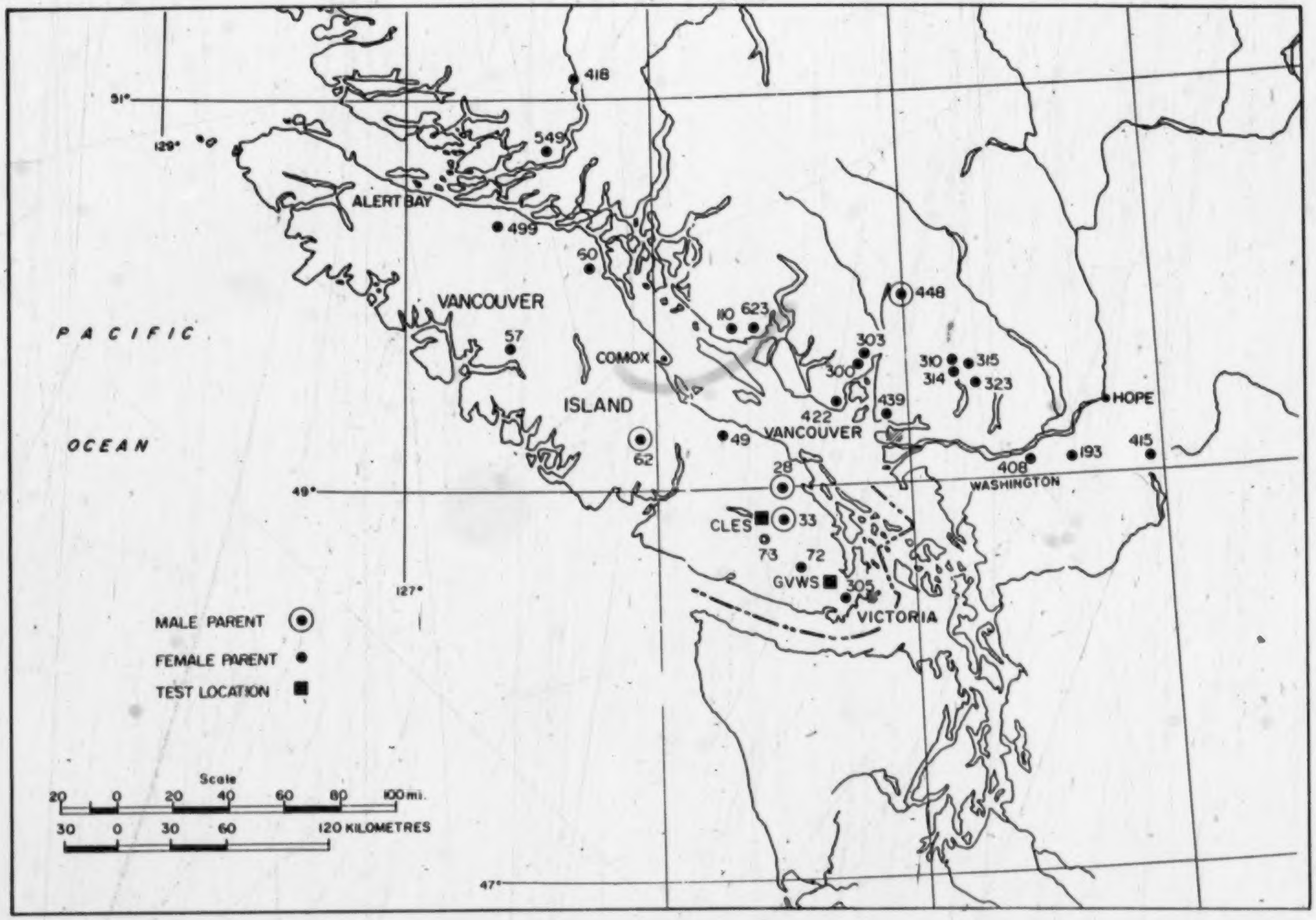
†B.C. plus tree registration number



PACIFIC
OCEAN
VANCOUVER
ISLAND
ALERT BAY
COMOX
VANCOUVER
VICTORIA
WASHINGTON
HOPE
418
549
499
50
57
62
110
623
49
303
300
422
439
448
310
315
314
323
408
193
415
28
33
CLES
73
72
GVWS
305
51°
129°
49°
127°
47°
MALE PARENT
FEMALE PARENT
TEST LOCATION
Scale
20 0 20 40 60 80 100 mi.
30 0 30 60 120 KILOMETRES

Figure 4. Geographic distribution of parent tree locations and test sites.

2.2 Statistical and Genetic Analyses

Analysis of variance was performed on the measurements for the purpose of testing hypotheses about the significance of family related effects and also for the purpose of estimating variance components for these effects. The analysis, for a random model, was conducted on individual trees using a least-square analysis of variance program for unbalanced data developed by F.C.H. Yeh (Technical Advisor Genetics, British Columbia Forest Service and Department of Forest Science, University of Alberta) and UANOVA, a general purpose analysis of variance program developed by T. Taerum (Computing Services, University of Alberta).

Variance components were estimated by equating the mean square for each effect with its expectation (Tables 2-4) and solving for the component (Appendix B). Standard errors of variance components were calculated as per Becker (1975) (Appendix B). Components of covariances among traits were calculated by using the variance component models (Tables 2-4) on the sum of the values for the pair of traits in question and solving for the covariance term (Kempthorne 1957:pg 264).

Assuming no linkage, epistasis, and inbreeding, the components of variance among females (σ_f^2) and males (σ_m^2) estimates one-quarter of the additive genetic variance (σ_A^2) (Hanover and Barnes 1962). In the "tester" mating design the selection unit and the source of information for additive genetic variance is the female seed tree parent (σ_f^2).

TABLE 2. Structure of analyses of variance and covariance on individual sites.

Source of variation	Degrees of freedom	Mean squares or mean cross products	Expected mean squares or mean cross products
Replications	r-1=2	MS_1	$\sigma_w^2 + k_1\sigma_{rmf}^2 + k_2\sigma_{rf}^2 + k_3\sigma_{rm}^2 + k_4\sigma_r^2$
Males	m-1=3	MS_2	$\sigma_w^2 + k_5\sigma_{rmf}^2 + k_6\sigma_{mf}^2 + k_7\sigma_{rm}^2 + k_8\sigma_m^2$
Females	f-1=21	MS_3	$\sigma_w^2 + k_9\sigma_{rmf}^2 + k_{10}\sigma_{mf}^2 + k_{11}\sigma_{rf}^2 + k_{12}\sigma_f^2$
Rep x males	(r-1)(m-1)=6	MS_4	$\sigma_w^2 + k_{13}\sigma_{rmf}^2 + k_{14}\sigma_{rm}^2$
Rep x females	(r-1)(f-1)=42	MS_5	$\sigma_w^2 + k_{15}\sigma_{rmf}^2 + k_{16}\sigma_{rf}^2$
Males x females	(m-1)(f-1)=63	MS_6	$\sigma_w^2 + k_{17}\sigma_{rmf}^2 + k_{18}\sigma_{mf}^2$
Plot	(r-1)(m-1)(f-1)=126	MS_7	$\sigma_w^2 + k_{19}\sigma_{rmf}^2$
Within plot	rmf(t-1)	MS_8	σ_w^2

Terms and components of variance explained in Table 4.

TABLE 3. Structure of analyses of variance and covariance on combined sites.

Source of variation	Degrees of freedom	Mean squares or mean cross products	Expected mean squares or mean cross products
Sites	s-1=1	MS_1	
Replications/sites	s(r-1)=4	MS_2	
Males	m-1=3	MS_3	$\sigma_w^2 + k_1\sigma_{rmf}^2 + k_2\sigma_{smf}^2 + k_3\sigma_{mf}^2 + k_4\sigma_{rm}^2 + k_5\sigma_{sm}^2 + k_6\sigma_m^2$
Females	f-1=21	MS_4	$\sigma_w^2 + k_7\sigma_{rmf}^2 + k_8\sigma_{smf}^2 + k_9\sigma_{mf}^2 + k_{10}\sigma_{rf}^2 + k_{11}\sigma_{sf}^2 + k_{12}\sigma_f^2$
Site × males	(s-1)(m-1)=3	MS_5	$\sigma_w^2 + k_{13}\sigma_{rmf}^2 + k_{14}\sigma_{smf}^2 + k_{15}\sigma_{rm}^2 + k_{16}\sigma_{sm}^2$
Site × females	(s-1)(f-1)=21	MS_6	$\sigma_w^2 + k_{17}\sigma_{rmf}^2 + k_{18}\sigma_{smf}^2 + k_{19}\sigma_{rf}^2 + k_{20}\sigma_{sf}^2$
Males × females	(m-1)(f-1)=63	MS_7	$\sigma_w^2 + k_{21}\sigma_{rmf}^2 + k_{22}\sigma_{smf}^2 + k_{23}\sigma_{mf}^2$
Rep × males	s(r-1)(m-1)=12	MS_8	$\sigma_w^2 + k_{24}\sigma_{rmf}^2 + k_{25}\sigma_{rm}^2$
Rep × females	s(r-1)(f-1)=84	MS_9	$\sigma_w^2 + k_{26}\sigma_{rmf}^2 + k_{27}\sigma_{rf}^2$
Site × cross	(s-1)(m-1)(f-1)=63	MS_{10}	$\sigma_w^2 + k_{28}\sigma_{rmf}^2 + k_{29}\sigma_{smf}^2$
Plot	s(r-1)(m-1)(f-1)=252	MS_{11}	$\sigma_w^2 + k_{30}\sigma_{rmf}^2$
Within plot	srmf(t-1)	MS_{12}	σ_w^2

Terms and components of variance explained in Table 4.

TABLE 4. Components of analyses of variance models.

Term

s = number of sites

r = number of replications within sites

m = number of male pollen trees

f = number of female seed trees

t = number of trees within plots

Variance components

σ^2_w = variance among trees within plots

σ^2_{rmf} = variance among full-sib family plots within sites

σ^2_{smf} = variance among site-male-female combinations

σ^2_{mf} = variance among male-female combinations

σ^2_{rf} = variance among rep-female combinations within sites

σ^2_{rm} = variance among rep-male combinations within sites

σ^2_{sf} = variance among site-female combinations

σ^2_{sm} = variance among site-male combinations

σ^2_f = variance among female half-sib families

σ^2_m = variance among male half-sib families

σ^2_r = variance among replications within sites

σ^2_s = variance among sites

k_i = coefficient of the "i"th variance component

The component of variance among full-sibs (σ^2_{mf}) estimates one-quarter of the dominance genetic variance (σ^2_D). Because of the small number of pollen parents (four), the precision for estimating dominance genetic variance with the tester mating design is low, especially for low heritability traits (Pederson 1972).

Genotype × environment interaction (G.E.I) sources of variation can be tested by using:

σ^2_{sf} for additive × environment interaction (σ^2_{AE}),
σ^2_{smf} for dominance × environment interaction (σ^2_{DE}).

2.2.1 Heritability and Selection Concepts

One of the most important genetic parameters used in evaluating the response to selection is heritability. Heritability has value primarily as a method of quantifying the concept of whether progress through selection for a character is relatively easy or difficult to make in a breeding program (Hanson 1963). At the basic level heritability is defined as the ratio of additive genetic variance (σ^2_A) to phenotypic variance (σ^2_{Pi}) (Falconer 1982). As a utility to a breeder, heritability statements should be unified with reference to a selection concept (Hanson 1963). The concept of heritability as a regression coefficient (Falconer 1982; Hanson 1963) is:

COV(phenotypes measured for selection, genotypes generated)

+

phenotypic variance of the mean value of the selection unit

is useful in forestry where the relationship between the selection unit and the improved generation may have many different permutations (Namkoong *et al.* 1966; Shelbourne 1969b; Namkoong 1979).

Where individuals measured from the progeny test are the selection unit, the phenotypic variance is expressed as:

$$\sigma^2_{Pi} = \sigma^2_A + \sigma^2_D + \sigma^2_{GxE} + \sigma^2_E \qquad 1$$

In terms of the variance components from the analysis of variance (Tables 2 & 3); this becomes:

$$\sigma^2_{Pi} = \sigma^2_m + \sigma^2_f + \sigma^2_{mf} + \sigma^2_{sm} + \sigma^2_{sf} + \sigma^2_{rm} + \sigma^2_{rf} + \sigma^2_{smf} + \sigma^2_{rmf} + \sigma^2_w \qquad 2$$

The numerator of the heritability is the covariance between the genetic value produced for utilization and the phenotypes measured to estimate that value. This covariance, when genotypes are produced from selected individuals, is that of offspring-parent ($\frac{1}{2}\sigma^2_A$). In mass selection where select trees freely intermate (Shelbourne 1969b, Namkoong 1979), this covariance is σ^2_A (because both parents are selected) and the full narrow sense heritability applies:

$$h_i^2 = \frac{\sigma_A^2}{\sigma_{Pi}^2} \qquad 3$$

In a breeding program, pedigree information can be used to assess more accurately an individual's breeding value than just its own performance, as in mass selection. This is especially helpful with characters of low heritability such as growth traits (Falconer 1982). Selection can be from the parent generation where the parent's progeny are used to derive the parent's breeding value. Recurrent selections can be made on individuals within the progeny test, using the performance of an individual's half- and full-sibs to aid in the definition of its breeding value.

The phenotypic variance of half- and full-sib family means is the phenotypic variance among half- or full-sibs, divided by the number of observations making up each kind of mean. For half-sibs, the phenotypic variance from our model (Table 3) is:

$$\sigma_{PHS}^2 = \sigma_f^2 + \frac{k_{23}}{k_{12}}\sigma_{mf}^2 + \frac{k_{20}}{k_{12}}\sigma_{sf}^2 + \frac{k_{27}}{k_{12}}\sigma_{rf}^2 + \frac{k_{29}}{k_{12}}\sigma_{smf}^2 + \frac{k_{30}}{k_{12}}\sigma_{rmf}^2 + \frac{1}{k_{12}}\sigma_w^2 \qquad 4$$

For full-sibs, the phenotypic variance from our model is

$$\sigma_{PFS}^2 = \sigma_m^2 + \sigma_f^2 + \sigma_{mf}^2 + \frac{k_{29}}{k_{23}}\sigma_{smf}^2 + \frac{k_{30}}{k_{23}}\sigma_{smf}^2 + \frac{1}{k_{23}}\sigma_w^2 \qquad 4$$

The "tester" mating design of this experiment is designed to test seed tree parents. The selection process is progeny testing, where the characteristics of progeny are used to assess the breeding value of their parents rather than the progeny themselves (Turner and Young 1969; Falconer 1982). Progeny tests can supply information about the breeding value of parents (the 22 seed tree parents) and genetic parameters for the parental population. The parameters derived from a progeny test thus refer to the parental population (the base population of select parent trees) rather than the progeny population. As pointed out by Falconer (1982) the concept of progeny-test selection can be confusing because of ambiguity about which generation is being selected, the parents or their progeny. Because this is a type of family selection, "family" and "progeny-test" selection will be used as equivalent terms in this study.

In the selection of the best parent trees based on their progeny's performance, the numerator of the heritability is the covariance between the phenotypes measured for selection (i.e., the progeny of the 22 seed tree parents) and genotypes generated for utilization (i.e., progeny of the selected trees). The relationship is thus that of half-sibs and the covariance between half-sibs is $\frac{1}{4}\sigma_A^2 = \sigma_f^2$. The heritability (family) for this selection becomes:

$$h_f^2 = \frac{\sigma_f^2}{\sigma_{PHS}^2} \tag{6}$$

Expected percentage gain from selecting the best parent trees is (Namkoong *et al*. 1966):

$$\begin{array}{r} \%\Delta G_f = i \times 2\ (h_f^2 \times \sigma_{PHS} \times 100) \\ X \end{array} \tag{7}$$

where X is the population mean. This can also be stated as:

$$\%\Delta G_f = i \times 2\ (h_f^2 \times CV_{PHS}) \tag{8}$$

where CV_{PHS} is the coefficient of variation of the half-sib phenotypic variance. The selection intensity "i", refers to how many standard deviations the mean of select parents are above the mean of the whole population. Response to selection can thus be expressed as percentage response per standard deviation unit of selection or per unit "i":

$$\%\Delta G_f/i = 2\ (h_f^2 \times CV_{PHS}) \tag{9}$$

The "2" is because select parent trees act as both male and females (clonal seed orchard) (Namkoong *et al*. 1966).

Recurrent selections involving second generation material are limited with the present mating design (NC II) because of the potential of inbreeding; only four unrelated second generation individuals can be selected from the entire planted stock. Thus simple recurrent selection (mass selection) or combined selection schemes are not compatible with the "tester" mating design of this study. Gain calculations from a simple recurrent selection (mass) within the progeny test are reported for comparison purposes and are calculated by:

$$\%\Delta G_i / i = h_i^2 \times CV_{Pi} \qquad 10$$

2.2.2 Correlation of Traits

The models developed for estimating genetic and phenotypic variances also apply to covariances. Genetic and phenotypic correlations between traits were also investigated as parameters. Phenotypic correlations were assessed for individuals, r_{Pi} (based on σ^2_{Pi} & COV_{Pi}), and for half-sib (female) families, r_{PHS} (based on σ^2_{PHS} & COV_{PHS}) (Appendix B). Genetic correlations, r_A, are the correlation of breeding values (Falconer 1982). Environmental correlations, r_E, are the correlations of environmental deviations together with the non-additive genetic deviations (Falconer 1982) (Appendix B). The standard error of r_A was calculated as per Falconer (1982) (Appendix B). Because variance estimation errors are multiplied in these parameters, they are most usefully interpreted with regard to general magnitude and sign. Correlated response to selection was investigated for several important characters according to the formulae of Falconer (1982) (Appendix B).

Path-coefficient analysis (Wright 1921, 1923) is a standardized partial regression analysis by which a model of cause-and-effect can be investigated (Kempthorne 1957; Li 1975). Campbell (1963) used a model of the cause-and-effect of the phenotypic relationships of crown characters on stem volume. Path-coefficient analysis was used to emulate this model, but instead of using phenotypic relationships, additive genetic relationships between traits were used. Path analysis was also used as a graphic aid to identify key crown traits for inclusion in multiple trait selection indices for the importance of their effects (direct and indirect) on stem volume.

2.2.3 Multiple Trait Selection

Selections will seek to improve multiple economically important traits. Several methods of multiple trait selection can be used by breeders. Tandem selection (Falconer 1982) involves improving traits separately over successive generations, but is not feasable in forest tree breeding because of the long generation intervals. Independent culling establishes acceptance levels for each trait and the set of individuals failing to achieve any or all of these levels is culled. The drawbacks to independent culling are that a large population needs to be screened if many traits are to be improved, and no account is taken of the interrelationship of traits.

Index selection, as developed by Smith (1936), and Hazel (1943), provides a linear function of an individual's phenotypic value for two or more traits (X_i), where each value is weighted by a coefficient (b_i) designed to maximize the correlation between the function and the individual's genetic worth. An individual's genetic worth is defined as an aggregate consisting of a linear function of the breeding values, g_i, of i=(1,2,...m) traits, weighted by the relative economic values, a_i, of those traits:

$$H = \Sigma a_i g_i \tag{11}$$

The least-squares partial regression coefficient (b_i) of H on X_i provides the weighting coefficient for the index I in the form:

$$I = \Sigma b_i X_i \tag{12}$$

The least-squares solution for the vector of regression coefficients **b** is equal to $\mathbf{P}^{-1}\mathbf{Ga}$, where **P** is the matrix of variances and covariances among the X_i, **G** is the matrix of covariances between X_i and g_i, and **a** is the vector of economic weights (Appendix B). The variance of the index, σ_I^2, is calulated as **b'Pb**, and the variance of H, σ_H^2, is calulated as **a'Ga**.

The gain in genetic value of each trait in the aggregate genotype (G_i) as a result of selection on the index is:

$$\Delta G_i = i(b'G_i)/\sigma_I \qquad 13$$

where i is the selection intensity and G_i is the i^{th} column in the G matrix or the row vector of genetic covariances between the i^{th} trait and each component trait in the index (Lin 1978). The correlation between I and H (r_{HI}) measures the ability of a given index function to model the actual value of an individual's genotype. This statistic is useful for evaluating the effectiveness of an index and is calculated by:

$$r_{HI} = \sigma_I/\sigma_H \qquad 14$$

The index used for multiple trait selections is a "progeny test index" designed to rank and select the best parents for a combination of traits. In the progeny test index, P is the phenotypic variance-covariance matrix of (female parent) half-sib family means (σ^2_{PHS} & COV_{PHS}). G is the genetic variance-covariance matrix of (female parent) family variance and covariance components (σ^2_f & COV_f) (Appendix B). Economic dollar equivalents for tree improvement traits are not known. Two approaches were made to this problem. The first was to design the index for the improvement of one trait (volume) as per Bridgwater (1972), Robinson *et al.* (1951) and Stonecypher (1970). The second was first assume all traits going into the index have equal value ($a_i=1$), and then change these values in relation to each other. Changes in the ranking of families that occur due to changes in different value weightings were observed. The response (both expected and that observed in the progeny test) to selections on these different rankings were empirically plotted. Sensitivity plots to different value changes were made to derive an optimum selection strategy (Arbez *et al.* 1974; Baradat 1982).

2.3 Measurement Methods

Traits of growth, form, and wood quality recorded in the progeny are given in Table 5. Metric measurements used to estimate traits of growth and form are represented schematically in Figure 5. Measurements were taken at the 3rd, 4th, 5th, and 6th whorls down from the current leader and in the associated stem segment above the branch whorl - given as whorl numbers 6 through 9 (Fig. 5).

Some of the stem and upper crown attributes recorded relied on subjective scoring methods, but most traits were derived from measurements.

TABLE 5. Traits of growth, form, and wood quality assessed.

Trait		units	CLES			GVWS			COMBINED	
			n.obs	mean	C.V.	n.obs	mean	C.V.	mean	C.V.
Growth										
HT06	height 6th growing season	cm	2310	113.56	25.43	2096	100.61	31.49	107.40	28.80
HT10	height 10th growing season	cm	2324	416.66	17.96	2034	325.20	27.65	373.97	25.14
HT12	height 12th growing season	cm	2296	647.64	13.70	1916	513.76	21.16	586.74	20.25
HTD	growth from 10th to 12th year	cm	2296	228.70	15.88	1916	187.32	21.68	209.88	20.73
DM06	diameter 6th growing season	mm	2310	21.00	24.88	2095	17.19	34.48	19.19	30.67
DM10	diameter 10th growing season	mm	2324	70.79	20.89	2034	52.79	30.26	62.39	28.51
DM12	diameter 12th growing season	mm	2296	86.31	14.58	1842	66.06	20.10	77.30	21.16
VOLM	volume measurement	dm^3	2277	16.14	45.02	1251	10.84	46.01	14.26	49.25
Form										
BN	branch number	no	2277	5.13	21.48	1251	5.73	22.51	5.34	22.59
BA	branch angle	°	2277	64.82	11.01	1251	67.43	10.40	65.74	10.95
BT	branch thickness	mm	2277	19.95	16.75	1251	18.51	15.67	19.44	16.80
BTT	branch/stem diameter ratio	%	2277	26.36	12.28	1251	28.94	11.80	27.28	12.92
BL	branch length	cm	2277	164.69	15.64	1251	139.57	14.09	155.78	17.10
BLT	branch length/total height 10	%	2277	39.59	11.57	1251	37.86	13.84	38.97	12.55
KI	knottiness index	%	2277	27.53	27.22	1251	38.48	26.83	31.41	32.07
TAPER	taper measurement	mm/m	2277	18.88	25.59	1251	19.27	24.83	19.01	25.33
SIN	stem sinuosity score	no	2285	72.47	172.26	1916	96.82	172.17	83.58	174.59
FORK	forking score	no	2285	25.69	201.53	1916	27.14	207.08	26.35	204.30
LAFL	lammas score	no	2285	13.57	309.45	1916	12.16	345.81	12.93	325.36
Wood Quality										
WD	wood density (5mm cores)	kg/m^3	2173	363.01	7.16					
PIN	Pilodyn pin penetration	mm	2173	167.04	12.33					

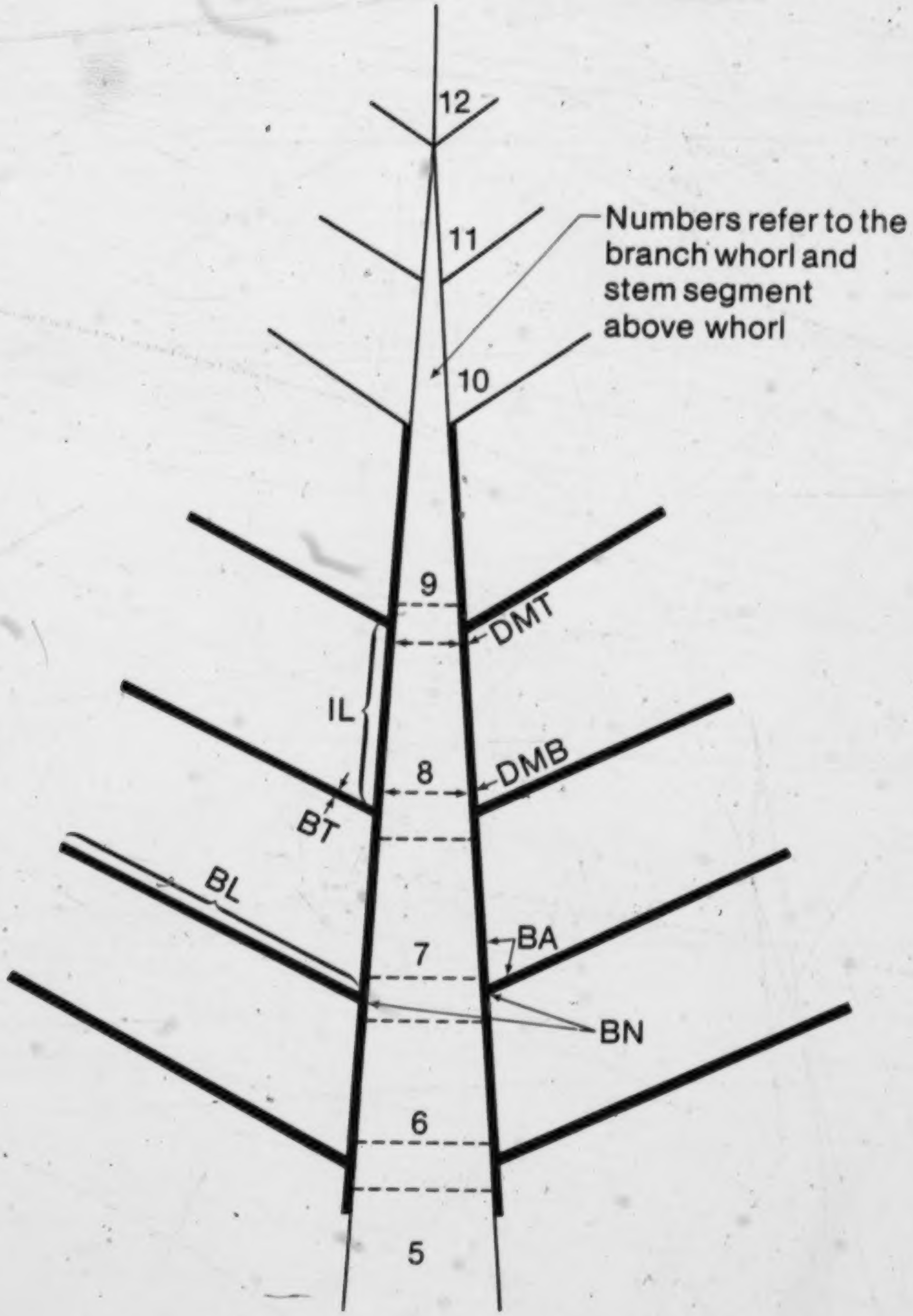

12
11
Numbers refer to the branch whorl and stem segment above whorl
10
9
DMT
IL
8
DMB
BT
BL
7
BA
BN
6
5

Figure 5. Schematic diagram of metric measurements made on the progeny trees.

2.3.1 Height and Growth Measures

Heights and diameters were recorded after the 6th, 10th and 12th growing season (*HT06*, *HT10*, *HT12*, *DM06*, *DM10*, *DM12*). Diameters were measured at a fixed reference height (Kovats 1977) except *DM12* , which was the mid-diameter measurement at the 7th interwhorl stem segment ((*DM7T*+*DM7B*)/2) (Fig. 5). *HTD* represented the growth of the trees from age 10 to age 12 (*HTD* = *HT12* - *HT10*).

Stem measurements made were (Fig. 5) of:

1. lengths of the inter branch-whorl stem segment, that is the stem length between each branch whorl (Internodal length *IL*) *IL9*, *IL8*, *IL7*, and *IL6* were measured where possible, and
2. outside bark diameters at the top and bottom of each stem segment (*DMT* & *DMB*). Measurements were recorded from the bottom of the ninth segment (*DMB9*) through to the top of the fifth segment (*DMT5*) depending on the size of the tree. Diameters were measured on the stem immediately above or below the swell of the branch whorl in the first area of clear stem wood below both primary and secondary branches (≈5cm).

From these detailed stem measurements, estimates of volume and taper were made. Volume (*VOLM*) was the accumulated volume of the stem segments as tapering cylinders plus the highest diameter to the top of the tree measured as a cone volume.

2.3.2 Stem Taper

Although taper is often taken as:

$$\text{TAPER} = \frac{\text{HEIGHT}}{\text{DM } 1.3}$$

or total height over diameter at 1.3 m (Jarret 1978), an actual taper measure could be made from the diameter measures taken down the stem (Fig. 5). Taper (*TAPER*) was simply the average taper of the stem segments ($\Delta DMB/IL$).

2.3.3 Metric Branch and Crown Form Traits

Branch measures were taken at the seventh, eighth and ninth whorls or the sixth, seventh, and eighth whorls, depending on the manageability of measuring branching characters on the ninth whorl of the tree. Seventh and eighth whorls were always recorded.

Branch numbers (*BN*) were counted in the same branching whorls. Two numbers were used; the first being all of the major branches within the whorl, the second was minor branches that lay just below the branch whorl by ≈5 cm.[*] The sum of these two numbers counts all branches between *DMB* of the stem segment above the whorl and *DMT* of the stem segment below the whorl. *BN* (Table 6) represents the average number of the seventh and eighth whorls.

---

[*] Douglas-fir does not have a definite whorl pattern, instead there often is a dominant upper portion of the whorl originating from one to five lateral buds immediately below the apical bud (major branches). A lower portion of the whorl may include branches that originate from lateral buds in the upper group of internodal buds (minor branches)(Campbell 1961). The differentiation between these types is not always clear.

Branch angle (*BA*) was measur~~ed~~ in the same branch whorls. Two randomly chosen major branches within the whorl were measured by protractor to the nearest 5°. *BA* (Table 5) represents the average angle of the seventh and eighth whorls.

Branch thickness (*BT*) was measured at two randomly chosen major branches in the whorl and measured in millimeters with calipers away from the swell where the branch joins the trunk (≈3 cm). *BT* (Table 5) represents a mean branch thickness from whorls seven and eight. *BTT* (Table 5) represents branch thickness of whorls seven and eight as a ratio of the stem diameter at the whorl:

$$BTT = \frac{BT}{DM}$$

where *DM* is the average of the diameter measured just above the whorl *DMB* and diameter measured just below the whorl *DMT*. This type of proportional branch thickness, that removes the size effect of the tree, was found to have a stronger genetic determination than direct branch thickness measures in Finnish Scots pine (Velling and Tigerstedt 1984). Campbell's (1961) measure of knottiness ratio (*KI*) - cross-sectional areas of branches at a whorl to the stem cross-sectional area - was calulated, this was derived using the mean branch thickness and branch number and the diameter value (*DM12*) for stem cross-section areas.

Branch length (*BL*) was measured at the same whorls. Two randomly chosen major branches within the whorl were measured to the nearest 5 cm. *BL* (Table 5) represents the average branch length of the seventh and eighth whorls. *BLT* (Table 5) represents branch lengths of whorls seven and eight as a ratio of the total height.

2.3.4 Stem and Upper Crown Form Attributes

Stem and upper crown form attributes recorded were sinuosity, forking (including ramicorn branching), and the occurrence of lammas growth (Table 5).

Measuring sinuosity in young plantations can be difficult and time consuming. Shelbourne and Namkoong (1965) and Campbell (1965) used photographic measures. Campbell (1965) used a transfomation of *h/a* (Fig. 2) from photographs as an objective measure of sinuosity, but found that a subjective scoring system could be quite reliable ($r=.76$, $P<.01$; for a sample of 30 trees). French studies (Crisan 1977) also demonstrated good correlations ($r=.98$, $P<.01$) between measured and subjective scoring methods for assessing straightness. Adams and Howe (1985) found that subjective scoring techniques were quite effective ($r=.79$, $P<.01$) and $r_A=.96$) compared to a scoring index based on numbers and frequencies of displacements from the vertical.

Sinuosity and the other attribute traits were all recorded using a similar subjective assessment technique. They were recorded by the stem segment or growing season in which observed, the severity of the damage to form observed on a scale of 1 to 5, and a diagnostic observation. The following traits were recorded:

2.3.4.1 Sinuosity

1st no. stem segment (growing season) of occurrence.

2nd no. severity score of stem damage;

1- slight occurrence or sinuosity trend,
displacement less than ½ of internode diam.

2- noticeable sinuosity,
displacement between ½-1 of internode diam.

3- marked sinuosity of a permanent nature,
displacement between 1-1.5 of internode diam.

4- severe sinuosity,
displacement between 1.5-2.0 of internode diam.

5- extreme sinuosity.
displacement > 2.0 of internode diam.

3rd Alpha observation;

J- sinuosity or crookedness was caused by damage or loss of apical leader.

SIN (Table 5) represents a total severity score for each tree ×100.

2.3.4.2 Forking, Ramicorn Branching, and Multiple Leader Occurrence

1st no. stem segment (growing season) of occurrence.

2nd no. severity score of stem damage;

1- slight occurrence or tendancy to occurrence

2- noticeable forking occurrence,

3- marked occurrence likely to be maintained, and damage stem quality,

4- severe occurrence,

5- extreme occurrence - competes equally for apical dominance with main leader.

3rd. Alpha observation;

F- forking,

R- ramicorn branch,

M- multiple leaders.

FORK (Table 5) represents a total forking severity score per tree where the score was ≥ 2 ×100.

2.3.4.3 Lammas Occurrence

1st no. stem segment (growing season) of occurrence.

2nd no. severity score of stem damage:

1- slight or unnoticeable occurrence,

2- noticeable occurrence but no upper stem damage,

3- marked occurrence - some upper stem damage presence of noticeable ramicorn branch or exceptional branchiness,

4- severe upper stem damage (usually forking),

5- extreme upper stem damage.

LAFL (Table 5) represents a total number of lammas occurrences of severity score ≥ 2 ×100.

2.3.5 Wood Density Traits

Wood density measurements were made only at CLES (Table 5). The trees in the watershed site (GVWS) were considered too small to sample for wood density. Two diametrically opposed 5 mm increment cores were taken from the first consistently clear stem segment above the base of each tree (*IL6*). Only the last four rings of each core were kept (years 8-12). Wood density (*WD*) was estimated by the maximum moisture content method (Smith 1954) with an assumed pycnometric density of 1500 kg/m^3. Samples with severe compression wood were excluded. Pilodyn estimation for wood density (*PIN*) was taken at *IL6* (approx. breast height) and consisted of two readings with a non-repeating Pilodyn of pin diameter 2.5mm and spring strength of 6 joules.

2.3.6 Transformations of Scale

There are three major reasons for making scale transformations: (1) to make the distribution normal, (2) to make the variance independent of the mean, and (3) to remove or reduce non-additive interactions (Falconer 1982). The major reasons considered with these progeny test traits were (1) and (2).

The attribute variables *SIN*, *FORK*, and *LAFL* show a markedly skewed distribution. The incidence of these attributes in the population is low and there are large ranges between families for these traits. The low incidence of these attributes in the population causes the distribution to approach a Poisson rather than a normal distribution, therefore a square-root transformation $X' = \sqrt{X + 1}$ would appear best (Montgomery 1984). The analysis was completed for transformed and untransformed data for the attribute traits.

3. RESULTS

3.1 Height and Growth and Yield Traits

Measurements reported in this chapter are total height at years 6, 10, and 12 (*HT06, HT10, HT12*); height accumulation between years 10 and 12 (*HTD*); diameters at years 6, 10, and 12 (*DM06, DM10, DM12*); and stem volume measurements (*VOLM*).

3.1.1 Height Traits

Early growth and site establishment was represented by height at six years (*HT06*). Trees at this age were slightly over 1 m (107 cm, CV=28.8%) tall with a range in family (female half-sib) means of between 92.6 cm to 118 cm (Table C1). Sources of variation for additive genetic variance (σ_A^2) were significant ($P<.05$) on the individual and combined site analyses (Table C2). The standard errors for σ_A^2 were less than half of the variances themselves.

Individual tree heritability levels were low, but for progeny test selection heritabilities were high. Heritabilities, coefficients of variation, and expected response to selection for height at age six (*HT06*) were:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_t^2	CV_{PHS}	$\%\Delta G_t/i$
0.14±0.06	28.00	3.86	0.73±0.31	6.10	8.87

(Table C2). Progeny test selection for early height growth should be effective in this population and nearly 9% gain per selection intensity unit is expected to be achieved.

Dominance genetic variance (σ^2_D) was non-significant for the early height trait; however, lack of precision for this non-additive source of genetic variance (because of only four male parents) is shown in the large standard errors (Table C2). Sources of variation for site*female and rep*female was non-significant, indicating that additive genetic × major environment interaction variances (σ^2_{AE}) are not important for this trait, within the limitations of these environments and experimental population.

Although σ^2_{sf} for early height growth (*HT06*) was non-significant, and significant rank changes did not occur between sites; the sites showed marked differences in their powers of genetic discrimination (Table C2). Additive genetic variance (σ^2_A) was most highly expressed at site GVWS, the slower growing site (Table C2). Coefficients of variation for phenotypic variances, σ^2_{Pi} and σ^2_{PHS}, were higher at GVWS, and response to selection was expected to be twice the level at GVWS as at CLES (Table C2). The coefficients of variation of the experimental error (within-plot (σ^2_w) and plot-to-plot error (σ^2_{rmf}) sources of variation) were slightly higher at GVWS than CLES. However, in proportion to the CV's of family sources of variation, they are 1.5 times higher at CLES than GVWS. The higher variance component percentage of σ^2_w at CLES (78.4% CLES, 71.4% GVWS; Table C2) indicates the possibility that the row plots of CLES may be less precise for determining genetic differences than the square plots at GVWS.

At height 10-years (*HT10*), the overall mean was 374 cm (CV=25.1%), and families ranged from 343 cm to 397 cm (Table C3). Additive genetic variance (σ_A^2) was a significant source of variation ($P<.05$) on the combined analysis (MS_{s*f} = error MS), but was non-significant ($P>.10$) at CLES. At GVWS it was non-significant ($P>.05$) for the random model, but was significant ($P<.05$) using MS_{m*f} as the error MS (replications as fixed effect).

Height measurement at 12 years (*HT12*) averaged nearly 6 m (587 cm, CV=20.2%) and families ranged from 546 cm to 620 cm (Table C5). The same trends of significance as with *HT10* were observed; the combined analysis was significant ($P<.05$), while CLES was non-significant ($P>.10$), and GVWS was marginal in its significance. Large standard errors of σ_A^2 ($\approx\sigma_A^2$) for these two later height measures (*HT10* and *HT12*) are present on individual sites, especially at site CLES, whereas on the combined analysis standard errors are less than one half of the variance components (Tables C4 & C6). Heritabilities are also more strongly expressed on the combined analysis than on the individual sites. Heritabilities and selection parameters for height at 10 years (*HT10*) and height at 12 years (*HT12*) on the combined analysis were:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV'_{PHS}	$\%\Delta G_f/i$
0.12±0.04	22.36	2.68	0.64±0.23	4.85	6.19
0.14±0.05	17.12	2.40	0.66±0.23	3.96	5.18

(Table C4, C6). A decline in expected percent response to selection as trees grow (*HT06*, *HT10*, *HT12*) is not brought about by declining heritabilities, but by declining coefficients of variation (of σ^2_{Pi} and σ^2_{PHS}). There is less relative variation between larger trees (≃6 m) than between smaller trees (≃1 m).

As with early height (*HT06*) the later height measures ~~*HT10* and *HT12* are non-sig~~nificant ($P>.05$) for dominance genetic variance (σ^2_{mf}) and G.E.I. sources of variation (σ^2_{sf} and σ^2_{rf}). However, they were significant ($P<.05$) for σ^2_{smf}.

The growth between *HT10* and *HT12* was examined in the trait *HTD* (*HTD* = *HT12* - *HT10*). There is some rationale for using this as a better trait for inherent growth rate differences than a single height measure. As height is cumulative, and the transplanting shock, growth check, and vegetative competition may effect the height of a tree for many years, the error that this is likely to introduce can be reduced by taking some multiple measure of heights or height differences as in *HTD*. An overall mean of *HTD*, of over 210 cm (CV=20.7%), shows the vigourous growth that is occurring at the plantation sites (CLES = 229 cm, GVWS = 187 cm) (Table C7). Family means over both sites range from

195 cm to 222 cm. Family differences are significant (P<.05) on both the combined analysis and for individual sites. *HTD* demonstrates itself as a more sensitive measure of inherent differences for growth rate than single height measures *HT10* or *HT12*, especially at CLES (Table C8). The improvement at GVWS is not as marked. However, at this site many of the trees are still in a state of growth check with the vegetative competition from broom, and with continued browsing. Heritabilities and expected response to selection for height differences (*HTD*) on the combined site analysis were:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
0.08±0.05	18.12	1.45	0.59±0.33	3.34	3.93

(Table C8). Although significance levels are improved over straight height measures (*HT10* and *HT12*), heritabilities are lower than the *HT10* and *HT12* measures. Thus the selection parameters are not encouraging for *HTD*. Non-additive genetic variances are not significant (P>.05) for *HTD*.

3.1.2 Comparisons with Published Heritabilities for Height

Campbell (1972) used height increment as a measure of height growth in full-sib seedlings of Douglas-fir. Campbell (1972) found significant amounts of both additive and dominance genetic variances for this measure. Unlike the factorial design Campbell's (1972) study study (NC I) has low reliability for differentiating these components and he suggested that the dominance effect was due to under estimation of the female effects which was part of the additive genetic variance. Campbell's (1972) report of a significant source of variation for additive genetic variance but low heritabilities (h_i^2 = 0.10-0.16) concurred with the results presented here.

In comparison with Rehfeldt's (1983) study of height in four year-old O.P. progeny of interior Douglas-fir, and published values from the French IUFRO provenance progeny values (Jarret 1978, Birot and Christophe 1983), the individual tree heritability values presented here are low:

Measurement	h_i^2	Reference
Height at 4yrs	0.52±0.10	Rehfeldt 1983
Height at 8yrs	0.36±0.19	Jarret 1978
Height at 12yrs	≃0.30	Birot and Christophe 1983
Height at 12yrs	0.14±0.05	Thesis results

Heritability estimates derived from open-pollinated families are biased when the assumption that the genetic covariance between O.P. progeny is that of half-sibs is violated (Namkoong 1966; Squillace 1974). Although Rehfeldt (1983) adjusted for an inbreeding coefficient of F=0.10 this bias may account somewhat for the differences between the O.P.

studies and the full-sib studies (Campbell 1972; Yeh and Heaman 1982). Family heritabilities between Rehfeldts (1983) study and the results presented here concur:

Measurement	h_f^2	Reference
Height at 4yrs	0.77±0.15	Rehfeldt 1983
Height at 6yrs	0.73±0.31	Thesis results

The testing environment and age of material are also important factors in the determination of environmentally sensitive traits such as height-growth. Nursery and farm field trials show higher heritabilities than progeny trials that simulate production plantations, and heritabilities for height growth can decline with age.

3.1.3 Trends in Components of Height Traits

Environmental influences and ecological conditions for growth change for a tree during its long life time. In early seedling stages it is dominated by vegetative competition from herbs and shrubs and influences of micro-climate and micro-site. Later as it dominates its immediate environment and it is influenced by only relatively large-scale climatic and site factors.

From their investigations of long-established progeny trials, Namkoong *et al*. (1972; for Douglas-fir) and Namkoong and Conkle (1976; for Ponderosa pine) recognized three broad ecological growth phases: early open growth to crown closure, a second phase after crown closure and the onset of intraspecific competition, and a third phase of growth indicating mature tree performance under stable cohort competition. Franklin (1979) and Cannell (1982) developed models of trends in the expression of additive genetic variances through the different growth stages. Franklin (1979) suggested that initial high levels of additive genetic variance that are expressed early in the juvenile growth period will decline as trees begin competing with each other. Cannell (1982) applied the concept of "isolation", "competition", and "crop" ideotypes[1] borrowed from the crop literature to these three growth phases. Cannell suggested that genotypes that do well in open-growth conditions, "isolation" ideotypes, can be quite different than those that do well in a competitive environment.

The time trend studies of Namkoong *et al.* (1972) and Namkoong and Conkle (1976) support the concept of consistent ideotype expression during specific ecological growth phases. Early stages showed positive and reasonable correlations of family effects during the period of open-growth. In the period of crown closure, 12-15 years for Douglas-fir, and 8-15 years for ponderosa pine, disruptions of these effects took place. High positive correlations were regained between measurements made in later growth phases. Both studies showed correlation of family effects between the open-growth phase and later growth phases to be non-existent or even negative.

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[1] "an ideotype is a biological model which is expected to perform or behave in a predictable manner within a defined environment" (Donald 1968)

Systematic and consistent trends of variance components over time have not always been observed. Lambeth *et al.* (1983) reported encouraging juvenile-mature correlations in Loblolly pine. The lack of significant family differences in the Douglas-fir study (Namkoong *et al.* 1972) and limitations in the design and objectives of these old studies, require that the interpretations made by Franklin (1979) and Cannell (1982) be approached cautiously.

Douglas-fir studies in France (Birot and Christophe 1983; Jarret 1978) indicated a sharp decline in the relative additive genetic variance after outplanting to age six and thereafter a leveling off or slight decline through the rest of the open-growth (juvenile) phase.

Trends in environmental and genetic variances as trees develop during this juvenile growth phase are shown by changes in variance component percentages and their coefficients of variation (CV). On the combined analysis the relative proportion of the variation attributable to site effects rises dramatically:

	HT06	*HT10*	*HT12*
σ_s^2	7%	36%	46%,

whereas the proportion attributable to within-plot variation declines sharply:

	HT06	*HT10*	*HT12*
σ_w^2	70%	45%	36%,

and the plot-to-plot variation declines slightly:

	HT06	*HT10*	*HT12*
σ_{rmf}^2	14%	12%	10%

(Tables C2, C4 and C6).

As trees become established on the sites during the juvenile growth phase, microsite influences are diminished and macroenvironmental influences become more important. The decline in the small-scale environmental effects as the trees grow from *HT06*≃1 m to dominating their local environment and filling the site (*HT12*≃6 m) is also shown by the decline in the coefficients of variation of the plot-to-plot (σ_{rmf}^2) and within-plot (σ_w^2) error variances, and the sources of variation of additive genetic variance (σ_f^2). This represents the fact that the scale of the overall variation within plantations declines as the trees get larger. The plantation now enters a stand growth model, where variation becomes more strongly expressed on a macro-environmental level, rather than the open-grown tree-to-tree growth model, where variation is relatively more expressed on micro-environmental level. The larger and faster growing trees (and families) are the first to be restricted by inter-tree competition as they reach the end of the juvenile growth phase. This allows the slower growing trees (and families) to catch up. On the combined analysis there is no decline in the relative proportion of additive genetic variance (σ_A^2) during the juvenile growth phase, but the height difference (*HTD*) does show a low heritability (h_i^2=0.08±0.05). On the individual sites there is a sharp drop between *HT06* and the later height measures, and there is a decline in the heritability values between site GVWS and site CLES. Because the trees are more developed and crown closure is almost complete at CLES, the trend of declining additive genetic variances during the juvenile growth phase may be more advanced there. But the imprecision of individual sites, especially CLES, may also be caused by the insensitivity of the experiment, in addition to biological models of declining genetic variances.

The experiment at CLES was restructured to see if specific sources of experimental error could be identified as causing the insensitivity at this site. The three major sources of environmental variation are the block or environmental variance (σ_r^2; which is usually removed before inferences about the population are made), the error variance of the large-scale environmental heterogeneity within blocks (σ_{rmf}^2; which is caused by the failure of the full-sib family plots to behave the same within environmental replications), and the error variance of small-scale environmental variation within plots (σ_w^2; which also has the remaining additive and non-additive genetic variation).

The large-scale experimental error (σ_{rmf}^2), can be reduced by reblocking the experiment based on plot performance. The CLES site occupies a long, thin parcel of land on an undulating topography of porous soils. Correct blocking of the experiment (LeClerg 1966) is difficult on such a site and re-analysis was made after the site was reblocked on ranking by plot means. Although plot variation (σ_{rmf}^2) declined from 19.4% to 1.1% (Table C9) of total variation, the significance levels of the female source of variation did not show an improvement in the estimate of additive genetic variatiance. In fact, estimates of heritability appropriate to mass selection had declined (h_i^2=0.05±.065; Table C9). Although this procedure restructured the blocks based on plot performance, the long, nine-tree row plots would appear to carry too much variability along with them to prove effective.

The experiment was also restructured to reduce σ_w^2 by taking sub-sets of the nine-tree plots. Analysis of the five top trees of each full-sib family plot showed a substantial increase for sources of variation of additive genetic effects (h_i^2=0.18±0.12) for height. This is brought about by the reduction of the within-plot variation (σ_w^2) from 69% (Table C9) to 36% and an increase of female variation (σ_f^2) to 4% of total variation. However, σ_f^2 was still non-significant (P>.05) and does not become significant until the plots are reduced to four-tree plots. At this reduction σ_f^2 = 5% of total variation and h_i^2=0.22±0.13).

The lack of sensitivity of the plantation to height growth may be accounted for by both a declining amount of additive genetic variance as slower starting families catch up (following the model of Namkoong *et al.* (1972) and Franklin (1979)), and microsite heterogeneity within the nine-tree row plots. Although microsite environmental influences decline as a proportion of the total variation, the decline is not large enough to offset the similar decline in the relative amount of additive genetic variance.

3.1.4 Diameter Traits

Diameter at the six-year measure had an overall mean of 19.2 mm (CV=30.7%) and a range in values between the female half-sib families of 16.4 mm to 21.8 mm (Table C10). Additive genetic variance was strongly expressed for this trait (5.820±2.132). Selection parameters for diameter at age six (*DM06*) were:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
0.19±0.07	28.84	5.48	0.77±0.28	7.18	11.00

(Table C11). Heritabilities and expected response to selection were higher for *DM06* than for *HT06*. As with height measures, other types of genetic variance (σ^2_{mf}, σ^2_{sf}) were non-significant.

At *DM12* the overall mean was 77.3 mm (CV=21.2%) and families range from 71.9 mm to 83.8 mm (Table C14). Selection parameters for diameters at ages 10 (*DM10*) and 12 (*DM12*) were:

h^2_i	CV_{Pi}	$\%\Delta G_i/i$	h^2_f	CV_{PHS}	$\%\Delta G_f/i$
0.16±0.06	24.72	3.96	0.75±0.26	5.73	8.55
0.16±0.06	16.94	2.79	0.73±0.25	4.03	5.85

(Tables C13 & C15). Heritability estimates for diameter measures were consistently higher than those of height measurements (Tables Appendix C). As with height measurements, heritabilities for diameter are lower than those published from the French IUFRO trials (Birot and Christophe 1983, $h^2_i \simeq 0.3$). A decline in percentage expected response to selection between *DM06* and *DM12* is caused by declining coefficients of variation. The trends in environmental influences that were observed for height measurement - a declining percentage of variation attributable to microsite influences (σ^2_w), and increasing influence of the macrosite (σ^2_s) - were also observed in the diameter traits.

Non-additive genetic variances were not significant (P>.05) for the two later diameter measures.

3.1.5 Volume Traits

Volume measurements were made on a reduced set of trees, only those that were not damaged by browsing or by competing vegetation. This mainly affected GVWS, where less than half of the trees had survived damage or mortality (see 2.1). The large replication (block) effect in the volume estimation (Table C17) represents a bias mainly attributable to survival and establishment at GVWS. Rep 1 is at the bottom of the slope where the soils are deeper and more moisture is available. A high incidence of broom in the replication has suppressed tree growth, and the nitrogen fixing ability of broom has likely made the trees more attractive to browsing animals. Although vigourous growth is observed in this rep, total mean height is in fact lower than in the other two reps because of these effects. The large mean for volume that was observed in this replication reflects the fact that trees were large enough to have escaped the influence of browsing and vegetative suppression and thus were measured for this trait (see also 3.2.2; Table 8).

The overall mean stem volume was 14.26 dm^3 (CV=49.2%), and families ranged from 11.24 dm^3 to 16.68 dm^3 (Table C16). Female half-sib families were a significant ($P<.05$) source of variation on the combined analysis ($\sigma_A^2 = 3.880 \pm 2.054$), and at GVWS, but not at CLES. Heritabilities and expected response to selection for stem volume (*VOLM*) on the combined analysis were:

h^2_i	CV_{Pi}	$\%\Delta G_i/i$	h^2_f	CV_{PHS}	$\%\Delta G_f/i$
0.10±0.05	44.76	4.26	0.55±0.29	9.32	10.25

(Table C17). Although the heritabilities for stem volume are lower than those for height and diameter, expected response to selection is higher because of the large half-sib phenotypic standard deviation (σ_{PHS}) of the volume measurements. Expected gains for progeny test selection are over 10% per selection intensity unit. Non-additive genetic variances were not significant (P>.05) for the volume measurement.

3.1.6 Selection of Height and Growth Traits

Genetic (r_A) and simple phenotypic correlations (r) between height and diameter measures are summarized in Table 6. All relationships are significant and positive. Detailed variances and covariances between traits *HT06*, *HT12*, *DM12*, and *VOLM* together with genetic (r_A), phenotypic (r_{Pi}, r_{PHS}) and environmental (r_E) correlations and direct and correlated response to selections are shown in Tables C18 to C21. These correlations are shown in Table 7. The correlation values between *HT06* and *HT12* (early and late height growth) are significant, positive, and of the same strong magnitude (≃.75). Between *HT06* and *DM12* (early height and late diameter growth) the correlations are not as strong as the height correlations and r_A and r_{PHS} are somewhat lower

($\simeq$.55) to r_E and r_{Pi} ($\simeq$.65). Between *HT12* and *DM12* (late height and late diameter growth) the genetic correlation r_A=.45±.21 and half-sib phenotypic correlation r_{PHS}=.58 have declined in relation to phenotypic (individual) and environmental correlation r_{Pi}=.81 and r_E=.88. The observed phenotypic correlations between later height and diameter measures indicate a greater influence due to the sharing of a common environment than do the earlier measures (Table 6).

Figure 6 represents expected response to mass and family selection (roguing of 1st generation clonal seed orchard) and correlated response for early selection for families at *HT06*. Expected response is shown by %ΔG / i for the four growth traits; *HT06*, *HT12*, *DM12*, and *VOLM*. It can be seen for all growth traits that family (progeny test) selection is more effective than mass selection for expected response from these traits. %*ΔG* was higher for volume because the multiplicative factors of the other growth measures in its determination increase the standard deviation accordingly. Early selection for families at *HT06* (age six: mean height $\simeq$ 1 m) proved reasonably effective for a correlated response at *HT12* (age twelve: mean height $\simeq$ 6 m) with relative efficiency R.E.= 77% and for *VOLM* (R.E.= 68%), but less effective with *DM12* (R.E.= 57%) (Fig 6).

TABLE 6. Genetic and simple phenotypic correlations between height and diameter measures and individual tree heritabilities.

	HT06	*HT10*	*HT12*	*DM06*	*DM10*	*DM12*
HT06	.14	.86	.73	.78	.84	.51
HT10	.79	.12	.98	.57	.76	.65
HT12	.73	.94	.14	.45	.63	.45
DM06	.86	.77	.72	.19	.90	.62
DM10	.81	.90	.86	.83	.16	.85
DM12	.63	.83	.87	.68	.88	.16

Above diagonal records genetic correlations.

Below diagonal records simple phenotypic correlations.

Along diagonal records individual heritability.

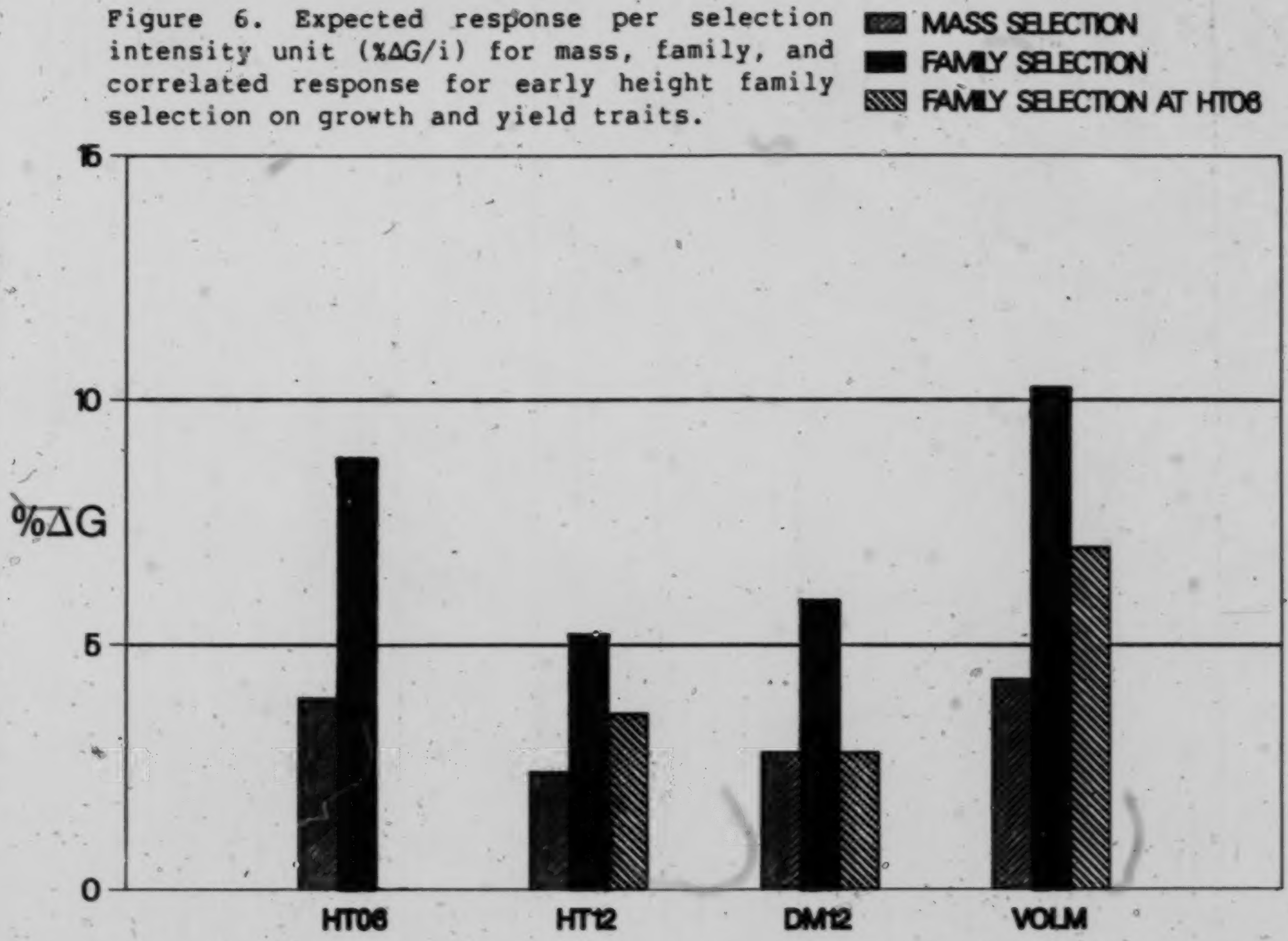
All terms significant P<.001

TABLE 7. Genetic, phenotypic, and environmental correlations between early height, later height and diameter, and volume traits.

		HT06	*HT12*	*DM12*
VOLM				
	r_A	.68±.21	.47±.28	.86±.09
	r_{Pi}	.80	.80	.88
	r_{PHS}	.74	.61	.92
	r_E	.81	.84	.89
DM12				
	r_A	.51±.20	.45±.21	
	r_{Pi}	.66	.81	
	r_{PHS}	.57	.58	
	r_E	.69	.88	
HT12				
	r_A	.73±.13		
	r_{Pi}	.75		
	r_{PHS}	.76		
	r_E	.76		

All terms significant $P<.001$

Figure 6. Expected response per selection intensity unit ($\%\Delta G/i$) for mass, family, and correlated response for early height family selection on growth and yield traits.



3.1.7 Index Selection for Volume and Response to Selection

Traits of height and diameter were investigated to look at the most effective way of selecting for volume. The trait *VOLM* as an actual measure of stem segment volume was seen as the "best" measure of stem volume. Estimates of *HT12* on its own, *DM12* on its own, and a multiple trait progeny test index, *IVOL*, of *HT06*, *HT12*, and *DM12* were analysed to predict the rankings of families based on *VOLM*. The index used the phenotypic variance-covariance matrix based on the heights and diameter (*HT06*, *HT12*, and *DM12*) and the additive genetic covariance of the heights and diameter traits to predict the breeding value of *VOLM*. The b_i's for *IVOL* were:

HT06	*HT12*	*DM12*
0.78	0.03	3.90

The coefficient of *HT12* ($\simeq 0$) shows that it has a negligible influence in predicting volume performance when used in conjunction with diameter and early height growth in the index and thus is a poor predictor of the breeding value of parents for stem volume.

Families were ranked by their phenotypic values for *VOLM* and the response was observed for selecting the top 50% of parents based on progeny performance (R_{OBS}). Comparisons were made of progeny gains for volume using selections on rankings based on the aggregate breeding value of the index

IVOL, and by indirect selection of volume using the individual growth traits (*HT12* and *DM12*). R_{OBS} at a selection level of 1:2 in dm^3, with the percent efficiencies compared to direct selection for volume on its own; the mean of the select progeny population (X) in dm^3; and Spearman rank correlation coefficients, r_s (Steel and Torrie 1980), of the family rankings based on the different selection criteria are:

	VOLM	*IVOL*	*DM12*	*HT12*
R_{OBS}	.881(100%)	.881(100%)	.816(93%)	.381(43%)
X =	15.114	15.114	15.049	14.614
r_s	1.000	0.988	0.889	0.553

The index values provide accurate weighting coefficients for selecting stem volume; however, selecting for diameter on its own is nearly as effective as selecting for volume measures using the index *IVOL* (93%). If a single character such as diameter can accurately predict the breeding values for the desired character, the inclusion of secondary characters in an index will give no real benefit; in fact, errors of estimation will make it more unreliable (Sales and Hill 1976; Falconer 1982). *HT12* on its own is not very efficient for predicting response for biomass (*VOLM*) (43%).

Observed response to selection from selected progeny families, R_{OBS}, can be compared to expected response *ΔG*. For fair comparisons the observed response was multiplied by two since expected response is calculated with the inclusion of a selected pollen source also. Values for a selection intensity of 1:2 or i=.77 were:

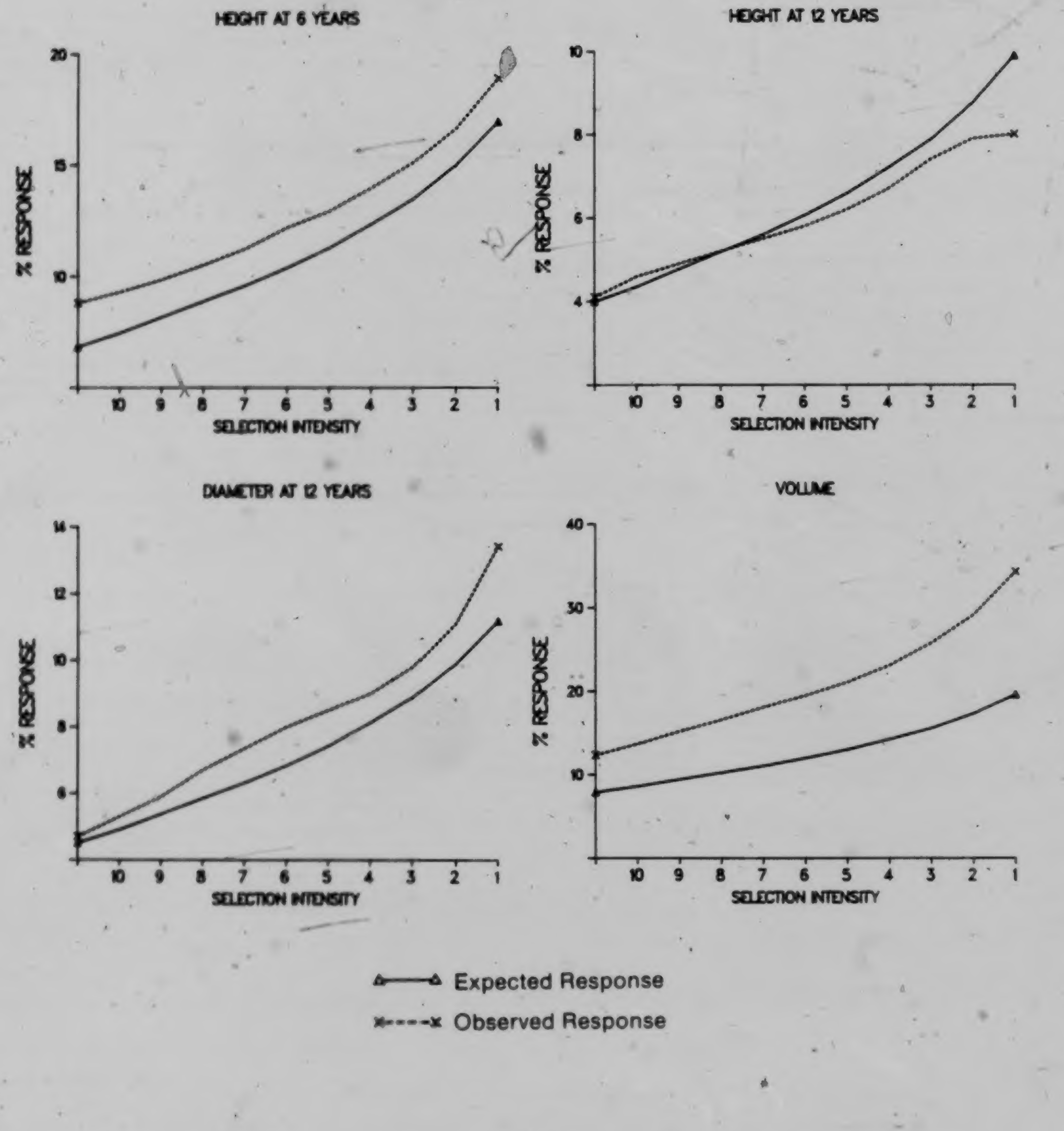
	HT06	*HT12*	*DM12*	*VOLM*
$\%R_{OBS}$	4.4 %	2.4 %	2.65%	6.2 %
$\%\Delta G$	3.4 %	2.0 %	2.25%	3.9 %

Values for a selection intensity of 4:22 or i=1.39 were:

	HT06	*HT12*	*DM12*	*VOLM*
$\%R_{OBS}$	7.0 %	4.1 %	5.75%	11.5 %
$\%\Delta G$	6.2 %	3.6 %	4.1 %	7.1 %

Observed (R_{OBS}) and expected (ΔG) response to selection for different selection intensity levels are plotted in Figure 7. Observed and expected response to selection are not independent, relying on the same progeny estimates; thus they agree quite well and gains from progeny test selection for yield trait appear quite reasonable (Figure 7). Observed response values were up to 75% higher than expected response to selection for this experimental population (Figure 7). This is in part due to the fact that the progeny were measured in family plots and shared a common environment.

Figure 7. Expected and observed response for growth and yield traits for increasing selection intensity on the 22 parent trees.



3.1.8 Height and Growth Summary

1. Sources of additive genetic variance (σ_f^2) were significant for height, diameter, and volume over combined sites. Dominance genetic variance was not significant (P>.05) for any of the growth traits. G.E.I. sources of variation (σ_{sf}^2) were non-significant for all traits. The source of variation for cross by site (σ_{smf}^2) was significant for later height measurements.

2. Individual tree heritabilites for growth and yield traits were low (0.08±0.05 - 0.19±0.07) but family heritabilities were high (0.55±0.29 - 0.77±0.28) for these traits. Individual tree heritability estimates were similar to published estimates from full-sib trials but were lower than estimates from open-pollinated trials. Family heritabilities were similar to reports published from O.P. trials. Heritability estimates were higher for diameter than height growth. With large phenotypic standard deviations, expected response to selection for the better parents in a clonal seed orchard appeared quite good ≈11% for diameter and volume traits (per unit of selection intensity).

3. As trees grow and dominate the site during the juvenile open-growth phase, microsite influences decline in relation to large scale macrosite influences. Trees are influenced more by large scale environmental factors than by other factors (including additive genetic variance) that influence tree to tree variation.

4. Individual sites were less accurate for demonstrating genetic differences. Heritabilities were lower on an individual site basis than for combined sites. Site CLES was especially insensitive, and later height and volume measures were non-significant ($P>.05$) at this site. Low heritabilites and non-significant sources of additive genetic variance for height and volume appeared in part to be due to the insensitivity of individual sites caused mainly by the heterogeneous environments within the nine-tree row plots (σ_w^2) at CLES.

5. Correlation of growth traits was good and correlated response for family selection for later height measures (*HT12* ≈6 m), diameter, or volume could well be made from early height measure (*HT06* ≈1 m).

6. Efficiencies for volume selections would best be made by selecting for diameter.

7. Both observed and expected responses to selection indicate reasonable gains can be achieved for yield traits.

3.2 Crown and Stem-Form Traits

Crown-form traits represent an average from branches at the fourth and fifth whorls (Fig. 5). Traits recorded were branch number per whorl (*BN*), branch angle (*BA*), branch thickness (*BT*), branch thickness as a ratio of branch diameter to stem diameter (*BTT*), branch length (*BL*), and branch length as a ratio to total height (taken at height age 10) (*BLT*).

Stem traits recorded were height at age 12 (*HT12*), diameter at age 12 (recorded in the fifth stem segment) (*DM12*), stem volume (*VOLM*), bole taper (*TAPER*); and stem form attributes including sinuosity (*SIN*), forking (*FORK*), and lammas flush (*LAFL*).

3.2.1 Branching and Crown Form Traits

Total branch number per whorl averaged 5.34 (CV=22.6%), and family means ranged from 4.8 to 6.0 (Table D1). Additive genetic variance was strongly expressed with a comparatively low standard error (σ^2_A=0.255±0.093) (Table D2). Female sources of variation accounted for over 4% of the total variation. The significant source of family variation for branch number contrasts to Jarret's (1978) work; he found branch number to be non-significant (P>.05). Non-significant results for branch number per whorl were also reported for white spruce (Merrill and Mohn 1985). However, studies on other species and populations have recorded significant sources of additive genetic variance for this trait in Scots pine (Poyko 1982; Velling and Tigerstedt 1984) and lodgepole pine (Cahman 1981; Rehfeldt 1985). Heritabilities, phenotypic coefficients of variation, and expected percent response to selection for branch number were:

h^2_i	CV_{Pi}	$\%\Delta G_i/i$	h^2_f	CV_{PHS}	$\%\Delta G_f/i$
0.19±0.07	21.76	4.10	0.82±0.30	5.21	8.56

(Table D2). Selecting the best parent trees for a seed orchard offers gains of over 8% per selection intensity unit. Non-additive genetic variances were non-significant (P>.05) for branch number (*BN*) (Table D2).

The overall mean for branch angle (*BA*) averaged on the fourth and fifth whorls was 65.7° (CV=11.0%), and family means ranged from 59.4° to 71.2° (Table D3). Family sources of variation were highly significant (P<.001) for branch angle on both the combined analysis and individual sites (Table D4). On the combined site analysis 16.3% of the total variation was attributable to family differences, making branch angle (*BA*) one of the most highly heritable traits in the study. Heritability and gain estimates were:

h^2_i	CV_{Pi}	$\%\Delta G_i/i$	h^2_f	CV_{PHS}	$\%\Delta G_f/i$
0.73±0.24	10.61	7.72	0.92±0.30	4.73	8.66

(Table D4). Individual tree heritability value is higher than the high values reported for coastal Douglas-fir populations in France (Jarret 1978, $h_i^2 = 0.54\pm0.23$; Birot and Christophe 1983, $h_i^2 = 0.49$). Moderate to high individual tree heritabilities have also been expressed in other conifers for branch angle (white spruce $h_i^2=0.44$, Merrill and Mohn 1985; Scots pine $h_i^2=0.43$, Poykko 1982; Scots pine $h_i^2=0.22\pm.09$, Velling and Tigerstedt 1984). The high individual tree heritability values and comparatively low uncontrolled within-family variation ($\sigma_w^2=62\%$) suggest that mass selection would be effective for improving branch angle in juvenile populations of coastal Douglas-fir. Additive genetic variance is not the only genetic variance source significant for branch angle; dominance genetic variance was also significant:

$\sigma_A^2 = 35.404\pm11.502$ $P<.001$

$\sigma_D^2 = 3.983\pm 2.009$ $P<.01$

(Table D4). Branch angle is one of the few traits for which this source of variation was significant; but even so this variation was only 10% of that of additive genetic variance. In a similar mating design for a similar set of traits in Scots pine, Velling and Tigerstedt (1984) reported branch angle as one of the few traits (out of thirteen) that was significant for dominance genetic variance.

Mean branch thickness (*BT*) was 19.44 mm (CV=16.8%), and family means ranged from 18.4 mm to 20.4 mm (Table D5). Branch thickness expressed as a percentage of branch diameter to stem diameter (*BTT*) averaged 27.28% (CV=12.9%), with a family range of 25.6% to 29.2% (Table D7). Family differences were non-significant ($P>.05$) for direct branch thickness measures (*BT*) on both individual and combined site (significance level .065, Table D6) analyses. Velling and Tigerstedt (1984) reported a non-significant heritability for branch thickness in Scots pine ($h_i^2=0.05$). However, significant heritability was reported by Jarret (1978; $h_i^2=0.34\pm0.18$) for Douglas-fir in France. The characterization of branch thickness as a percentage of branch diameter to stem diameter (*BTT*) was a much more sensitive indicator for family differences to branch size ($P<.001$); heritabilities were:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
0.26±0.10	11.64	3.04	0.78±0.31	3.36	5.27

(Table D8). Velling and Tigerstedt (1984) showed similar results in Scots pine, where branch thickness expressed as a ratio to stem diameter, was more sensitive for genetic discrimination than direct branch measures ($h_i^2=0.17\pm0.14$).

Mean branch length (*BL*) was 155.8 cm (CV=17.1%), and family means ranged from 143.4 cm to 165.3 cm (Table D9).

Branch length expressed as a percentage of branch length to height at age 10 (*BLT*) averaged 39.0% (CV=12.6%), with a family range of 37.2% to 41.6% (Table D11). Although branch length on its own was significant (P<.05) and selection parameters were:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
0.11±0.06	15.64	1.68	0.52±0.27	3.56	3.68

(Table D10), the ratio of branch length to total height was a more sensitive indicator of family differences (P<.001) and selection parameters were more favourable:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
0.19±0.07	11.80	2.22	0.77±0.30	2.93	4.48

(Table D12). Velling and Tigerstedt (1984) found similar relationships with Scots pine for crown width (branch length); crown width h_i^2=0.26±0.18, crown width/total height h_i^2=0.31±0.20.

Branch size traits may be better characterized in terms of proportioning of biomass between stem and branches than by direct branch growth measures.

3.2.2 Stem Form Traits and Attributes

Height, diameter and volume traits were described in the chapter on growth and yield (Table C1-C17). Taper estimates averaged 19.01 mm/m (CV=25.3%) in the population, and families ranged from 16.3 mm/m to 20.6 mm/m (Table D13). Sources of variation for additive genetic variance were significant (P<.01), and selection parameters from the population were:

h^2_i	CV_{Pi}	$\%\Delta G_i/i$	h^2_f	CV_{PHS}	$\%\Delta G_f/i$
0.10±0.05	25.70	2.53	0.57±0.30	5.35	6.08

(Table D14). Stem taper is thus an effective trait for progeny test selection, and gains of 6% per selection intensity unit is expected. Dominance genetic variance was significant for taper (P<.05) but was not as strongly expressed as additive genetic variance:

$\sigma^2_A = 2.352 \pm 1.246$ $P<.01$

$\sigma^2_D = 1.761 \pm 0.846$ $P<.05$

(Table D14). Other genetic effects were non-significant.

There was a wide range in family means for stem sinuosity score, ranging from 37.04 to 180.83, with an overall mean of 83.58 (CV=175%) (Table D15). A square root transformation was applied to the data to reduce its non-normality. For most data interpretations non-transformed data was robust because of the large data set used. Selection parameters for sinuosity on a non-transformed and transformed basis were:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
0.25±0.09	175.21	43.73	0.86±0.30	47.15	81.42
0.26±0.09	34.41	8.97	0.86±0.30	9.45	16.34

(Table D16). Although the scale effect of the distribution shows an exaggerated expected response to selection, the transformation demonstrates that family selection against this trait should be quite effective. Moderate to high heritability estimates for selections against sinuosity have been demonstrated in other studies on juvenile Douglas-fir:

h_i^2	0.52±0.23	Jarret 1978
h_i^2	0.39	Birot and Christophe 1983
h_f^2	0.5	Adams and Howe 1985.

These authors also suggest that family selection will be the most effective way of improving sinuosity. Non-additive genetic variances were non-significant for sinuosity.

Forking occurrence in the population was also highly skewed in its distribution (most trees having no forks). The trait *FORK* counts only those forks (including ramicorn branches and multiple leaders) that are noticeable and are likely to persist (score greater than or equal to 2). The overall population mean (multiplied by 100) was 26.35 (CV=204%), and families ranged from 10.26 to 45.11 (Table D17). Although the female source of variation accounted for only 1.9% of the total, it was a significant source of variation ($P<.05$). Selection parameters for forking (non-transformed and transformed) were:

h^2_i	CV_{Pi}	$\%\Delta G_i/i$	h^2_f	CV_{PHS}	$\%\Delta G_f/i$
0.08±0.03	207.20	15.98	0.66±0.27	35.32	46.86
0.08±0.03	19.06	1.49	0.66±0.27	3.28	4.33

(Table D18). The significant source of additive genetic variance for this trait in juvenile Douglas-fir presents a different result than that of the French provenance-progeny trials (Jarret 1978; Birot and Christophe 1983) where it was found to be non-significant ($P>.05$). Although the individual tree heritability value is low, progress through progeny test selection could be expected. The high within-family variance percentage (σ^2_w=83%) indicates much of the variation is uncontrollable, and phenotypic selection is unlikely to be useful.

Lammas growth or late season flushing (Fig. 3) is a major cause of forking and multiple leader formation (Rudolph 1964). It is an important trait to consider under form characteristics. The trait lammas flush (*LAFL*) is a count of the occurrences of lammas growth ×100. The overall population mean was 12.93 (CV=325%), and families ranged from 2.23 to 32.07 (Table D19). Sources of variation for additive genetic variance were significant for this trait ($P<.01$). Although only 2.6% of the total sources of variation are attributable to the selection source (σ_f^2), selection parameters indicate progress through parent tree selection is possible. Parameters for non-transformed and transformed lammas score were:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
0.11±0.05	331.84	34.73	0.62±0.28	68.38	84.28
0.10±0.05	15.47	1.60	0.61±0.28	3.19	3.88

(Table D20). *LAFL* was significant for sources of variation for dominance genetic variance (σ_{mf}^2).

3.2.3 Observations on Components of Form Characteristics

In the section on trends in components of height traits (3.1.2) it was shown that as trees grow and establish themselves on sites, microenvironmental influences (σ_w^2) decline and trees are influenced more by large-scale environmental effects (σ_s^2). These large-scale environmental effects would include length of growing season, late season moisture availability, etc. - effects that are felt over a large scale and are cumulative over seasons. For many of the stem-form-attribute traits specific environmental effects appear most influential as causes of variation. Table 8 shows replication means for the juvenile stem-form-attribute traits at the Greater Victoria watershed site (GVWS). Replication 1 at GVWS shows high incidences - almost twice the site average - of juvenile growth-form features of sinuousity, forking, and lammas growth. Rep. 1 on the lower portion of the site has a high cover of broom, a nitrogen fixing species. High soil nitrogen, together with good late-season soil moisture availability on the lower part of the site, are strong causative factors of these types of growth disturbance features (De Champs 1978, Carter *et al.* 1985). Growth disturbance features appear to be affected by more specific features of the environment than are growth traits.

TABLE 8. Means and standard deviations for several growth and form traits by replication on the Greater Victoria Watershed Site.

	REPLICATION					
	1		2		3	
TRAITS	mean	S.D.	mean	S.D.	mean	S.D
HT12	507.19	115.88	509.56	98.87	525.38	109.94
VOLM	13.84	5.06	8.22	3.67	11.38	4.88
SIN	114.44	190.22	87.10	142.46	88.14	162.16
LAFL	16.26	46.43	8.60	34.46	6.75	31.00
FORK	39.36	65.87	21.51	49.91	19.93	48.56

3.2.4 Relationships Between Crown Form Characteristics

Simple correlation coefficients between crown and growth characteristics for individual sites and combined analyses are presented in Table 9. The major associations are those related to size of the tree (e.g., branch thickness and volume). Partial correlation coefficients controlling the effect of size (volume) are presented in Table 10. Consistent significant relationships similar to Campbell's (1963) study of phenotypic correlations in the branch and upper-crown attributes of Douglas-fir were:

1. trees with fewer branches have more acute angles,
2. trees with fewer branches have thicker branches,
3. trees with fewer branches have proportionaly longer branches,
4. acute-angled branches are thicker,
5. acute-angled branches are longer, and
6. thicker branches are longer, even accounting for volume.

Although the correlations are not strong enough to have one or a few of the traits explain the majority of the variation in others, there is a significant association of high branch numbers, comparitively light branching (thickness and length), and high branch angle. The contrasting association in form is for few but heavy and acute-angled branches.

Detailed variances, covariances and correlations among crown traits and between crown traits and growth traits are presented in appendix tables D21 to D26. The genetic relationships are summarized in Table 11.

TABLE 9. Simple correlation coefficients between growth and crown form traits on individual and combined sites.

		PEARSON CORRELATION COEFFICIENTS								
	HT12	DM12	VOLM	TAPER	BN	BA	BT	BTT	BL	BLT
HT12	CLES	.79 ***	.81 ***	-.17 ***	.07 **	-.08 ***	.71 ***	-.05 **	.77 ***	-.31 ***
	GVWS	.72 ***	.80 ***	-.19 ***	.30 ***	-.03	.62 ***	-.16 ***	.73 ***	-.35 ***
	BOTH	.81 ***	.83 ***	-.18 ***	.03 *	-.13 ***	.69 ***	-.22 ***	.80 ***	-.22 ***
DM12	CLES		.88 ***	.05 **	.12 ***	-.04 *	.78 ***	-.09 ***	.80 ***	-.06 **
	GVWS		.86 ***	.07 ***	.25 ***	-.11 ***	.79 ***	-.29 ***	.77 ***	-.01 NS
	BOTH		.88 ***	.03 *	.01 NS	-.14 ***	.77 ***	[illegible]31 ***	.84 ***	.05 **
VOLM	CLES			.04 *	.06 ***	-.07 ***	.81 ***	-.10 ***	.82 ***	-.11 ***
	GVWS			.03 NS	.33 ***	-.10 ***	.77 ***	-.28 ***	.75 ***	-.18 ***
	BOTH			.02 NS	.04 *	-.14 ***	.80 ***	-.26 ***	.83 ***	-.06 ***
TAPER	CLES				.04 *	-.09 ***	.12 ***	.15 ***	.07 ***	.36 ***
	GVWS				.00 NS	-.06 *	.10 ***	.04 NS	.00 NS	.26 ***
	BOTH				.03 *	-.07 ***	.10 ***	.11 ***	.03 NS	.31 ***
BN	CLES					.08 ***	-.02 NS	-.10 ***	.05 **	-.04 *
	GVWS					.11 ***	.12 ***	-.21 ***	.19 ***	-.23 ***
	BOTH					.13 ***	-.03 NS	-.04 **	-.03 NS	-.16 ***
BA	CLES						-.13 ***	-.14 ***	-.11 ***	-.01 NS
	GVWS						-.20 ***	.01 NS	-.12 ***	-.11 ***
	BOTH						-.19 ***	-.02 NS	-.17 ***	-.07 ***
BT	CLES							.40 ***	.86 ***	.09 ***
	GVWS							.17 ***	.78 ***	.08 **
	BOTH							.22 ***	.83 ***	.12 ***
BTT	CLES								.17 ***	.23 ***
	GVWS								-.04 NS	.05 *
	BOTH								-.07 ***	.09 ***
BL	CLES									.22 ***
	GVWS									.15 ***
	BOTH									.25 ***

*, **, ***= significant at .05, .01, .001 levels of probability.

TABLE 10. Partial correlation coefficients between crown form traits controlling for volume on individual and combined sites.

		BA	*BT*	*BTT*	*BL*	*BLT*
BN	CLES	.08 ***	-.12 ***	-.09 ***	.00 NS	-.04 *
	GVWS	.15 ***	-.23 ***	-.13 ***	-.10 ***	-.19 ***
	BOTH	.13 ***	-.10 ***	-.04 *	-.11 ***	-.16 ***
BA	CLES		-.12 ***	-.15 ***	-.08 ***	-.01 NS
	GVWS		-.19 ***	-.02 NS	-.07 **	-.14 ***
	BOTH		-.13 ***	-.06 ***	-.11 ***	-.08 ***
BT	CLES			.82 ***	.59 ***	.31 ***
	GVWS			.63 ***	.48 ***	.35 ***
	BOTH			.74 ***	.48 ***	.28 ***
BTT	CLES				.44 ***	.22 ***
	GVWS				.27 ***	.00 NS
	BOTH				.27 ***	.07 ***
BL	CLES					.56 ***
	GVWS					.44 ***
	BOTH					.54 ***

*, **, ***= significant at .05, .01, .001 levels of probability.

TABLE 11. Genetic (r_A) and phenotypic (r_{PHS}) correlations between crown form traits and genetic (r_A) correlations between crown form traits and yield traits.

	BN	*BA*	*BT*	*BTT*	*BL*	*BLT*
BN	.19	.19	.16	-.59	.18	-.11
BA	.37	.73	-.05	-.29	-.10	.12
BT	.22	-.23	.05	.38	.33	.11
BTT	-.46	-.25	.33	.26	-.04	.14
BL	.27	-.16	.66	.01	.11	.61
BLT	-.07	.00	.22	.06	.46	.19
HT12	.26	-.03	-.03	-.31	.38	-.59
DM12	.67	.18	.21	-.82	.22	.21
VOLM	.71	.18	.29	-.75	.28	-.19

Between crown form traits only:

above diagonal records genetic correlations,

diagonal records individual tree heritabilities,

below diagonal records phenotypic correlations of half-sib, family means.

Of the aforementioned relationships of crown character, the strongest genetic basis appears to be that between branch number (*BN*) and branch thickness as a proportion of stem thickness (*BTT*) (r_A=-0.59±0.18). Thus the contrast between trees with many but light branches could be utilized effectively for selection. Branch angle shows a moderate, negative genetic relationship (r_A=-0.29±0.23) with proportional branch thickness, further supporting the genetic association of these form types. Similar relationships are documented in white spruce (Merril and Mohn 1985) and Scots pine (Poykko 1982; Velling and Tigerstedt 1984).

The genetic relationships between branch form associations and yield were investigated through path-coefficient analysis. Path-coefficient analysis is a standardized, partial regression analysis that provides a method by which direct and indirect components of an association can be segregated (Wright 1923, Li 1975). The additive genetic relationships of branch traits can thus be evaluated for their direct and indirect influences on yield. The model of cause and effect of crown characters on yield is used to emulate the model of Campbell (1963), except that additive genetic relationships are used. Path analysis is also used as a graphic aid to select key traits for multiple trait selection for form and growth characters. By this method the influences (direct and indirect) of crown traits on yield can be visualized. The analysis consists of the simultaneous solution of the five following equations that provide all possible direct and indirect relationships among yield and crown variables (Fig. 8):

$$r_{15} = P_{15} + r_{12}P_{25} + r_{13}P_{35} + r_{14}P_{45} \qquad 1$$

$$r_{25} = P_{25} + r_{12}P_{15} + r_{23}P_{35} + r_{24}P_{45} \qquad 2$$

$$r_{35} = P_{35} + r_{13}P_{15} + r_{23}P_{25} + r_{34}P_{45} \qquad 3$$

$$r_{45} = P_{45} + r_{14}P_{15} + r_{24}P_{25} + r_{34}P_{35} \qquad 4$$

$$1 = P_{15}^2 + P_{25}^2 + P_{35}^2 + P_{45}^2 + 2r_{12}P_{15}P_{25} + 2r_{13}P_{15}P_{35} + 2r_{14}P_{15}P_{45} + 2r_{23}P_{25}P_{35} + 2r_{24}P_{25}P_{45} + 2r_{34}P_{35}P_{45} + P_{x5}^2 \qquad 5$$

Results using the direct measurements for branch thickness and branch length are presented in Table 12. Stem volume is affected mainly by the number of branches ($P_{35}^2 = .416$). Other effects are minor in comparison, and it can be seen that they affect volume through the indirect effect of branch number. The residual variation leaves nearly 45% of the variation unexplained by these traits.

The second analysis (Table 13) used the proportional branch measure traits (%) to predict volume. In this analysis proportional branch thickness (*BTT*) has at least as important a direct effect on volume as does branch number. These traits also have a strong indirect influence on each other. Branch number (*BN*) and proportional branch thickness (*BTT*) together account for 42% (P_{15}^2=.165, P_{35}^2=.257) of the genetic differences in stem volume by their direct influences; this is less than the 60% for phenotypic relationships found by Campbell (1963). Branch angle and proportional branch length do not have an important effect on stem volume. The additive genetic relationships between branch angle and branch length with both branch number and proportional branch thickness mean that selecting for high branch number and light branching will also improve branch angle and branch length.

A positive association of the good form complex with growth characters is encouraging, and the promotion of more branches per whorl will be less detrimental compared to the relative reduction of branch size, flatter branch angle and increased volume. The negative phenotypic relationship of *BA* with the growth traits (Table 9) was not noted in the genetic correlations. Jarret (1978) noted a very strong positive genetic correlation between vigour (height) and branch angle (r_A=0.96). Observations of a positive relationship between volume and a similar complex of form characters was found in Scots pine by Velling and Tigerstedt (1984). They concluded that the proportional branch diameter was of great importance for wood quality, and more than offset the promotion of branch number.

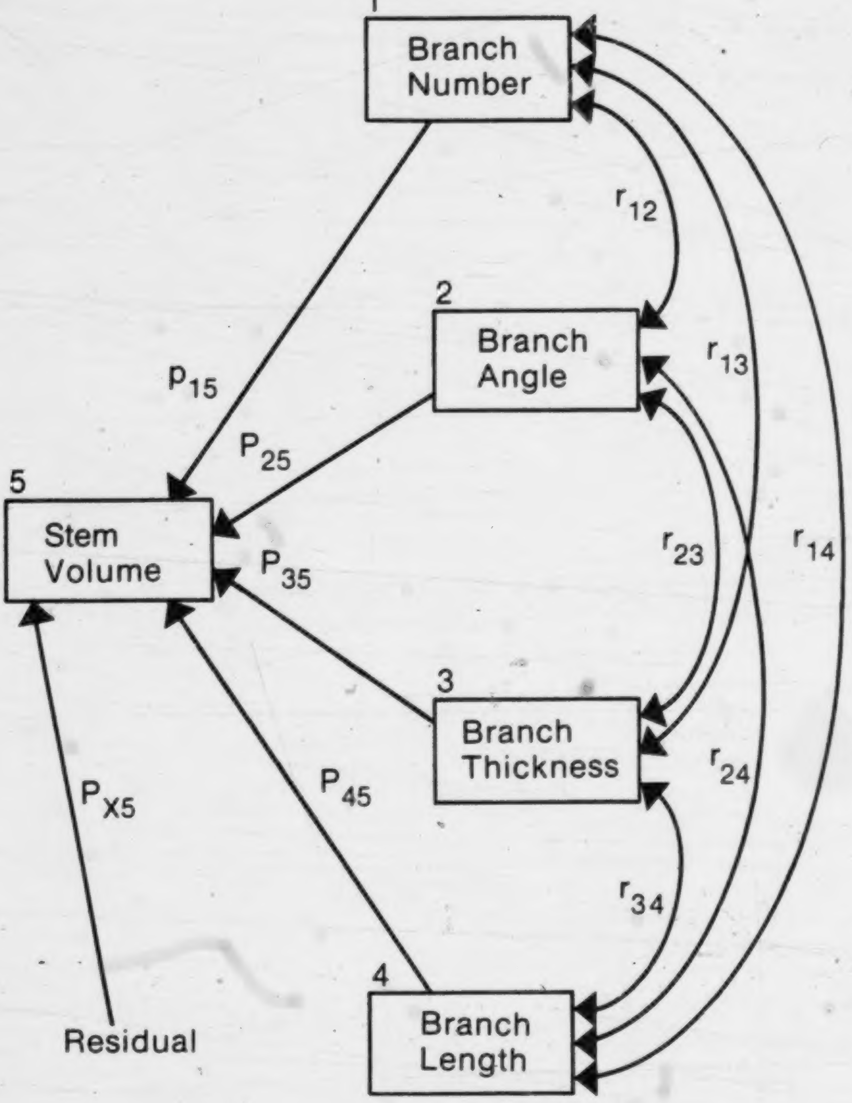

1
Branch Number
2
Branch Angle
3
Branch Thickness
4
Branch Length
5
Stem Volume
Residual
P_{15}
P_{25}
P_{35}
P_{45}
P_{X5}
r_{12}
r_{13}
r_{14}
r_{23}
r_{24}
r_{34}

Figure 8. Model of path-coefficient analysis of the association of crown form traits with stem volume.

TABLE 12. Path-coefficient analysis of the direct and indirect genetic associations of crown variables with stem volume.

	Crown Variables				
	BN	*BA*	*BT*	*BL*	*X*
Due to direct effect:					
P_{-5}	.645	.074	.140	.128	.675
Due to indirect effects:					
via branch number					
P_{15}		.123	.106	.114	
via branch angle					
P_{25}	.014		-.004	-.008	
via branch thickness					
P_{35}	.023	-.007		.047	
via branch length					
P_{45}	.023	-.013	.044		
Totals (additive genetic correlations)					
	.705	.177	.286	.282	

TABLE 13. Path-coefficient analysis of the direct and indirect genetic associations of crown variables with stem volume using proportional branch measures.

	Crown Variables				
	BN	*BA*	*BTT*	*BLT*	*X*
Due to direct effect:					
P_{-5}	.406	-.038	-.507	-.073	.575
Due to indirect effects:					
via branch number					
P_{15}		.077	-.239	-.044	
via branch angle					
P_{25}	-.007		.011	-.004	
via branch thickness					
P_{35}	.299	.146		-.072	
via branch length					
P_{45}	.008	-.008	-.010		
Totals (additive genetic correlations)	.705	.177	-.746	-.193	

3.2.5 Relationships With Stem-Form Traits

Correlations between bole taper and growth and yield traits, and between bole taper and crown-form traits are summarized in Table 14. Genetic correlations, more than phenotypic correlations, reflect that taller trees are less tapering, and trees of wider girth and greater stem volume are stronger tapering. Although the estimate of r_A was weak and non-significant between *DM12* and *TAPER* (r_A = 0.15±0.34), the correlation between *DM10* and *TAPER* (not shown) was strong (r_A = 0.53±0.28). Much of the volume of the stem is in the lower portion. Selection of trees for total height, without a measure of girth, will favour a less tapering bole at the expense of stem biomass. Strong, positive genetic correlations also exist between branch number and taper (r_A = 0.57±0.21), and branch thickness and taper (r_A = 0.73±0.28). These strong correlations reflect the partitioning of wood into branch material down the stem of the tree; higher-tapering trees having more and thicker branches.

Simple correlations between the stem attribute traits and growth traits are presented in Table 15. Consistent significant relationships were found that demonstrate:

1. taller trees are more sinuous,
2. trees of larger girth are more sinuous,
3. trees with a higher incidence of lammas growth are more prone to have forks and multiple leaders.

A significant negative correlation between *HT12* and *FORK* on site GVWS demonstrates the effect of rep 1 - reduced total cumulative growth and a high incidence of growth disturbance features (Table 8).

Phenotypic (r_{Pi}, r_{PHS}), genetic (r_A), and environmental (r_E) correlations between stem attributes and growth traits are presented in Table 16. With the replication effect removed, the negative relationship between forking incidence and height is removed, although the tendency of a negative but non-significant genetic correlation (r_A=-0.17±0.27) is still aparent.

The major significant stem-attribute relationship with growth is that between stem sinuosity and height growth (r_A=0.41±0.21). The relationship is large enough to indicate that selection for height on its own will increase the occurrence of sinuosity in the population. These results corroborate the high genetic (r_A=0.63) and significant phenotypic correlations between height and sinuosity that were found by Jarret (1978). Results from the study population indicate that this genetic relationship is non-significant for sinuosity and stem diameter (r_A=-0.13±0.25). The phenotypic (individual) and environmental correlation between diameter and sinuosity (r_{Pi}=0.23, r_E=0.33; Table 16) suggest that individual trees of larger girth are taller. In terms of selection, diameter selections are less likely to increase the occurrence of sinuosity than height selections.

TABLE 14. Phenotypic, genetic, and environmental correlations between taper and growth traits, and taper and crown form traits.

	HT12	*DM12*	*VOLM*
TAPER			
r	-.18 ***	.03 *	.02 NS
r_A	-.38±.31	.15±.34	.17±.36
r_{Pi}	-.18	.07	.04
r_{PHS}	-.27	.16	.14
r_E	-.16	.06	.02

……………………………………………

	BN	*BA*	*BT*	*BTT*
r	.03 *	-.07 ***	.10 ***	.11 ***
r_A	.57±.21	-.05±.29	.73±.19	.26±.30
r_{Pi}	.08	-.08	.11	.12
r_{PHS}	.40	-.12	.52	.28
r_E	.00	-.14	.07	.10

*, **, ***= significant at .05, .01, .001 levels of probability.

TABLE 15. Simple correlation coefficients between stem attribute and growth traits on individual and combined sites.

		DM12	*SIN*	*FORK*	*LAFL*
HT12	CLES	.79 ***	.21 ***	.10 ***	.04 *
	GVWS	.82 ***	.30 ***	-.21 ***	-.07 **
	BOTH	.87 ***	.17 ***	-.04 *	.00 NS
DM12	CLES		.18 ***	.17 ***	.08 ***
	GVWS		.29 ***	-.09 ***	.01 NS
	BOTH		.13 ***	.05 **	.05 ***
SIN	CLES			.00 NS	-.03 NS
	GVWS			-.03 NS	-.03 NS
	BOTH			-.02 NS	-.03 NS
FORK	CLES				.36 ***
	GVWS				.48 ***
	BOTH				.41 ***

*, **, ***= significant at .05, .01, .001 levels of probability.

TABLE 16. Phenotypic, genetic, and environmental correlations between stem attribute traits and growth traits on the combined analysis.

		SIN	*FORK*	*LAFL*
HT12				
	r_A	.41±.21	-.17±.27	-.14±.31
	r_{Pi}	.28	-.04	-.02
	r_{PHS}	.33	-.04	-.00
	r_E	.25	-.02	-.00
DM12				
	r_A	-.13±.25	-.14±.27	-.10±.31
	r_{Pi}	.23	.07	.06
	r_{PHS}	-.10	.02	.10
	r_E	.33	.09	.08

3.2.6 Growth and Crown Form Selections

The selection process summarized in this chapter is designed to improve traits of growth and yield, and form simultaneously. The growth trait chosen was stem diameter (*DM12*), because it is an easy trait to measure, and as has been shown, it is an accurate response variable for predicting stem volume. Crown form traits were chosen for their ease of measurement, for the likely effectiveness of their response (as demonstrated by their genetic parameters), for their value considerations, and for their genetic correlations with other traits in the fine-branching form type. Three selection schemes were investigated:

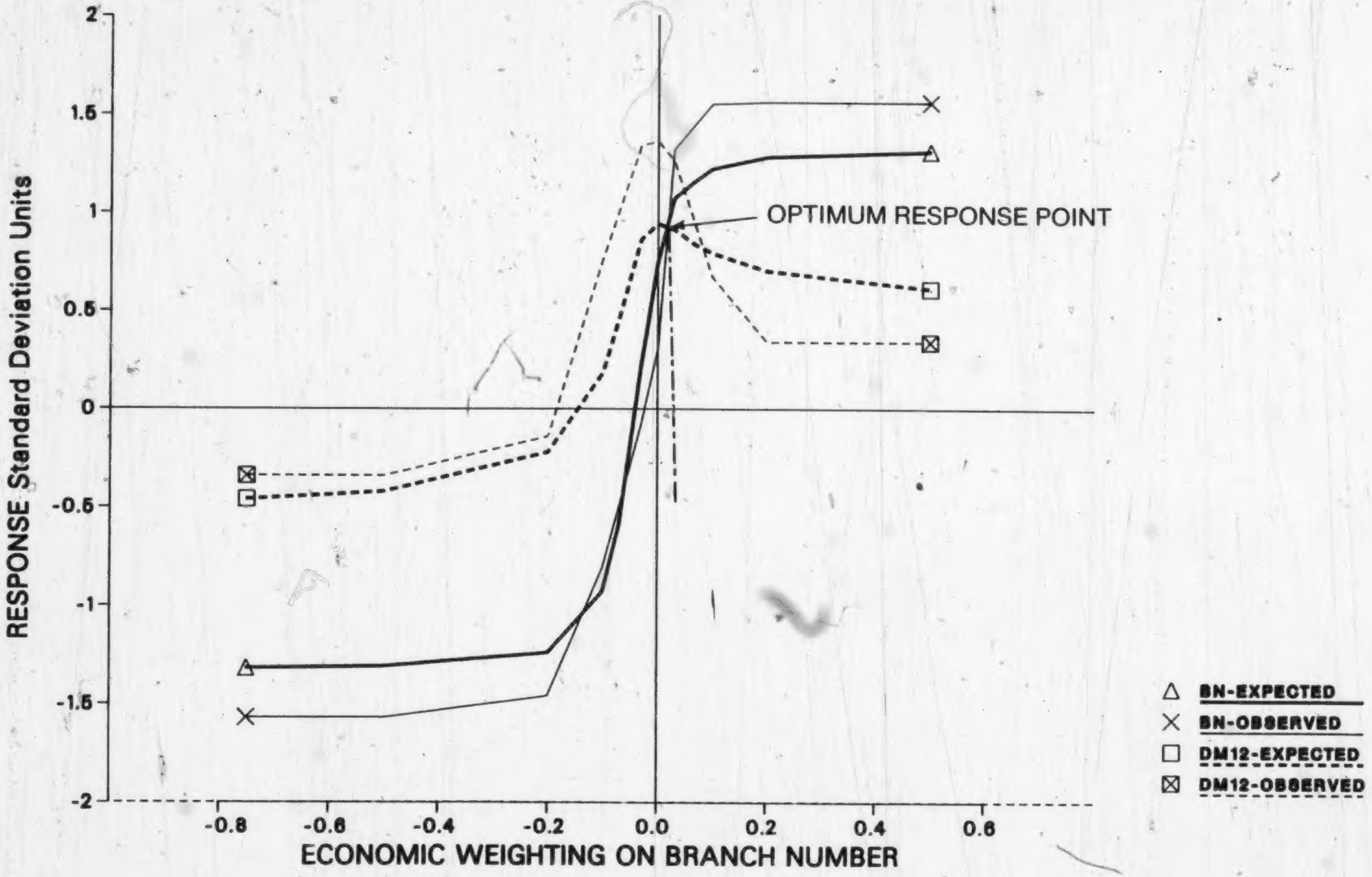
1. a multiple trait index that selects for diameter and branch number (*IBN*),
2. a three trait index that selects for diameter, branch number, and against proportional branch thickness (*IBNT*),
3. selection using the composite trait of knottiness index (*KI*).

The growth and form indices developed here seek to improve the net genetic worth of the aggregate genotype (H). Correct evaluations of H requires economic weights for each trait. Since true dollar values for growth and form traits are uncertain for Douglas-fir, the economic weights of *BN* in relation to *DM12* were changed over the range of +1 to -1 (for the first index *IBN*, of *BN* and *DM12*) and the primary objective of these selection indices became one of making empirical choices based on the estimation of genetic gains of individual traits. The response of each trait of the index for the different rankings that occur for changing economic weights is plotted in Figure 9. Both observed (R_{OBS}) and expected (ΔG) responses to selection were plotted for a selection intensity of 1:2 and were expressed in standard deviation units (R_{OBS} was multiplied by two because the pollen parent should also be selected). The optimum point for selection when economic weights are highly uncertain is where each trait is maximized for its minimum expected gain, at the curve intersection points (Namkoong 1979). The optimum response point in the *IBN* index is at a value weighting of .03 for *BN* and 1.0 for *DM12* (Fig. 9). The b values for *IBN* at the 0.03:1.0 value ratio were:

DM12	*BN*
0.49	0.03

At this optimum level the response level (R_{OBS}) for *DM12* is .628/.681=92% of the level of direct selection for *DM12* on its own, and *BN* is .661/.783=84% of its maximum response for this selection intensity. Although the maximum response of each trait is not achieved by this strategy, there is little loss from the maximum achievable response because of the strong positive genetic correlation between traits and this genetic association has been strengthened.

Figure 9. Response curves (R_{OBS} and ΔG) for branch number and diameter holding the economic weight of diameter at one and changing the weight on branch number, *IBN*.



Because of the positive association of the fine-branching form type (profuse, light, excurrent branching) the response (R_{OBS}) of the other form traits to *IBN* selections is also favourable. Branch angle is improved by .26/.81=32% of the direct selection level at the optimum level of *IBN* at the 1:2 selection intensity levels. Proportional branch thickness is reduced by .39 of a standard deviation unit or .39/.77=50% of the level that would be achieved through direct selection against *BTT* on its own. The correlation between the index (I) and its genetic worth (H), r_{HI}, for the changing values ranged from 0.8 to 1.0 and averaged 0.9; thus indicating the relative efficiency of the index *IBN*.

The second index used *BTT* along with *BN* and *DM12* in a multiple trait progeny test index of crown form and yield. The sensitivity plotting of this index (*IBNT*) to changing economic weights is too complex to plot effectively, but an iterative process was used to find the maximin (Namkoong 1979) point where response of each trait in the index (R_{OBS}) were approximately equal. Economic values (a_i), b values (b_i), R_{OBS} values, and comparisons with direct selection for the trait on its own (relative efficiencies), are shown for this index:

	DM12	*BN*	*BTT*
a_i	1.00	0.03	-0.01
b_i	0.45	0.07	-0.23
R_{OBS}	0.62	0.61	-0.51
R.E.(R_{OBS})	0.91%	0.78%	0.66%

The optimum strategy here is to maximize the minimum response to each trait; by losing only 10% of our efficiency in selecting for yield on its own, and 20% - 30% for the other traits, selections enforce the associations in the fine-branching form type.

In both of these indices the empirically derived optimum response levels are better when crown traits are valued low (≈0) compared to the yield trait. This emphasizes the positive association of yield and crown form traits. Crown form traits are improved strongly through their genetic covariances with traits of yield.

Another way of selecting crown form is to select against the composite trait of knottiness index (*KI*) (Campbell 1961; Jarret 1978). The overall mean for (*KI*), the average of the ratio of total branching surface area to stem surface area was 31.4% (CV=32%), and family means ranged from 25.8% to 34.8% (Table D27). Family sources of variation were significant (P<.01) and heritability and gain estimates were:

h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
0.16±0.07	21.82	3.38	0.69±0.32	5.16	7.15

(Table D28). Although not significantly different, heritability values were not as high as reported for coastal Douglas-fir populations in France (Jarret 1978, $h_i^2 = 0.29 \pm 0.16$). Details of the analyses of covariance of *KI* with the other important form traits are presented in Appendix Tables D29-D33. The relative efficiencies (R.E.) of these form traits, to correlated response to progeny test selection against *KI* were:

	DM12	*BN*	*BT*	*BTT*	*BA*
R.E.	34%	-33%	-77%	-50%	8%

It can be seen that selecting against the composite trait *KI* improves branch thickness and diameter but does not promote the profuse and flat-branching form type.

3.2.7 Crown and Stem Form Summary

1. Sources of variation for additive genetic variance (σ_f^2) were significant ($P<.05$) for all 11 crown and stem form traits, except branch thickness, on the combined analysis. Sources of variation for dominance genetic variance (σ_{mf}^2) were significant for branch angle, bole taper, and lammas occurrence only; and even so the estimates of dominance genetic variance for these significant traits were much less than the estimates of additive genetic variance. G.E.I. sources of variation ($\sigma_{sf}^2, \sigma_{smf}^2$) were not significant for any trait.

2. Branch angle should respond well to mass selection ($h_i^2=0.73\pm0.24$) as has been reported in other studies. The other form traits would respond best to family selection. Moderate heritability ($h_i^2\geq0.2$) was found for branch number, proportional branch thickness, proportional branch length, and sinuosity. Branch thickness and branch length as direct growth measures; and bole taper, forking, and lammas occurences all had low heritabilities ($h_i^2\approx0.1$).

3. Branch thickness and branch length were best measured as proportional traits - branch thickness as a proportion to stem thickness at the measuring point, and branch length as a proportion of total height.

4. There was an association among high branch number, light branch size (thickness and length), and high branch angle - in contrast to low branch number, heavy branch size (thickness and length) and acute-angled branches. Genetic

relationships were established for a fine-branching form type and were shown to be positively associated with yield.

5. Path-analysis showed that branch number and proportional branch thickness were associated with 42% of family differences for stem volume.

6. Negative genetic correlations were demonstrated between height and bole taper. Strong positive genetic correlations exist between bole taper and branch number, and bole taper and branch thickness. Bole taper is thus implicated in the shifting of woody material from the bole to the branches.

7. There was a positive association between stem sinuosity and individual growth traits, especially height growth. Genetic correlations suggest that height selections will promote sinuosity whereas diameter selections will not. This corroborates the finding of Jarret (1978).

8. Multiple trait selection for the improvement of form and growth traits can accentuate the positive association of the fine-branching form type of profuse/light/excurrent branches with stem volume. Selecting key traits in the form complex (branch number and proportional branch thickness) along with stem diameter can favourably affect all traits. Selecting against a composite trait of branch/stem surface ratio can improve form but is not as effective as multi-trait selection for promoting the fine-branching form type.

3.3 Wood Quality Traits

Traits reported in this chapter were wood density, estimated using the maximum moisture content method on the outer 4 rings of two 5 mm cores (*WD*), and a wood density estimate using the resistance of wood to a non-repeating Pilodyn pin (*PIN*). Wood density measures were only made at the Cowichan Lake site (CLES).

3.3.1 Wood Quality Traits

Wood density measures averaged 363.01 kg/m^3 (CV=7.16%), and family means range from 339.5 to 382.8 kg/m^3 (Table E1). Additive genetic variance was strongly expressed, with a comparatively low standard error (σ^2_A=572.32±181.20) (Table E2). Female sources of variation were significant (P<.001) and accounted for over 20% of the total. The individual tree heritability value for wood density (*WD*) was high (h^2_i =0.90±0.28); the highest value in this study. The low comparative error of within-family variation (σ^2_w=54%) suggests this trait should respond well to mass selection. Selection parameters for wood density (*WD*) were:

h^2_i	CV_{Pi}	$\%\Delta G_i/i$	h^2_f	CV_{PHS}	$\%\Delta G_f/i$
0.90±0.28	6.97	6.23	0.93±0.30	3.41	6.37

(Table E2). The high individual tree heritability agrees with values for wood mean density from 14-year-old coastal

Douglas-fir provenance-progeny trials in France (most provenances > 0.8; Bastien *et al.* 1985). In spite of the strong individual tree heritability, large percentage gains in wood density from progeny test selection cannot be expected because variation between family means was not large (CV_{PHS}=3.4). Sources of variation for dominance genetic variance (σ^2_{mf}) and G.E.I. variance (σ^2_{rf}) were non-significant for wood density.

Pin penetration averaged 16.7 mm (CV=12.3%), and family means ranged from 14.9 mm to 18.5 mm (Table E3). Family sources of variation were highly significant (P<.001). Heritability estimates were comparable to those found from the cores. Selection parameters for *PIN* were:

h^2_i	CV_{Pi}	$\%\Delta G_i/i$	h^2_f	CV_{PHS}	$\%\Delta G_f/i$
0.81±0.26	12.06	9.71	0.90±0.29	5.72	10.23

(Table E4). The value of *PIN* for predicting genetic differences as demonstrated by the high heritability estimates is in contrast to the results of Bastien *et al.* (1985), whose heritability estimates for the Pilodyn were low. Unlike the *WD* value, dominance genetic variance for the Pilodyn measure (*PIN*) was significant (P<.01; Table E4).

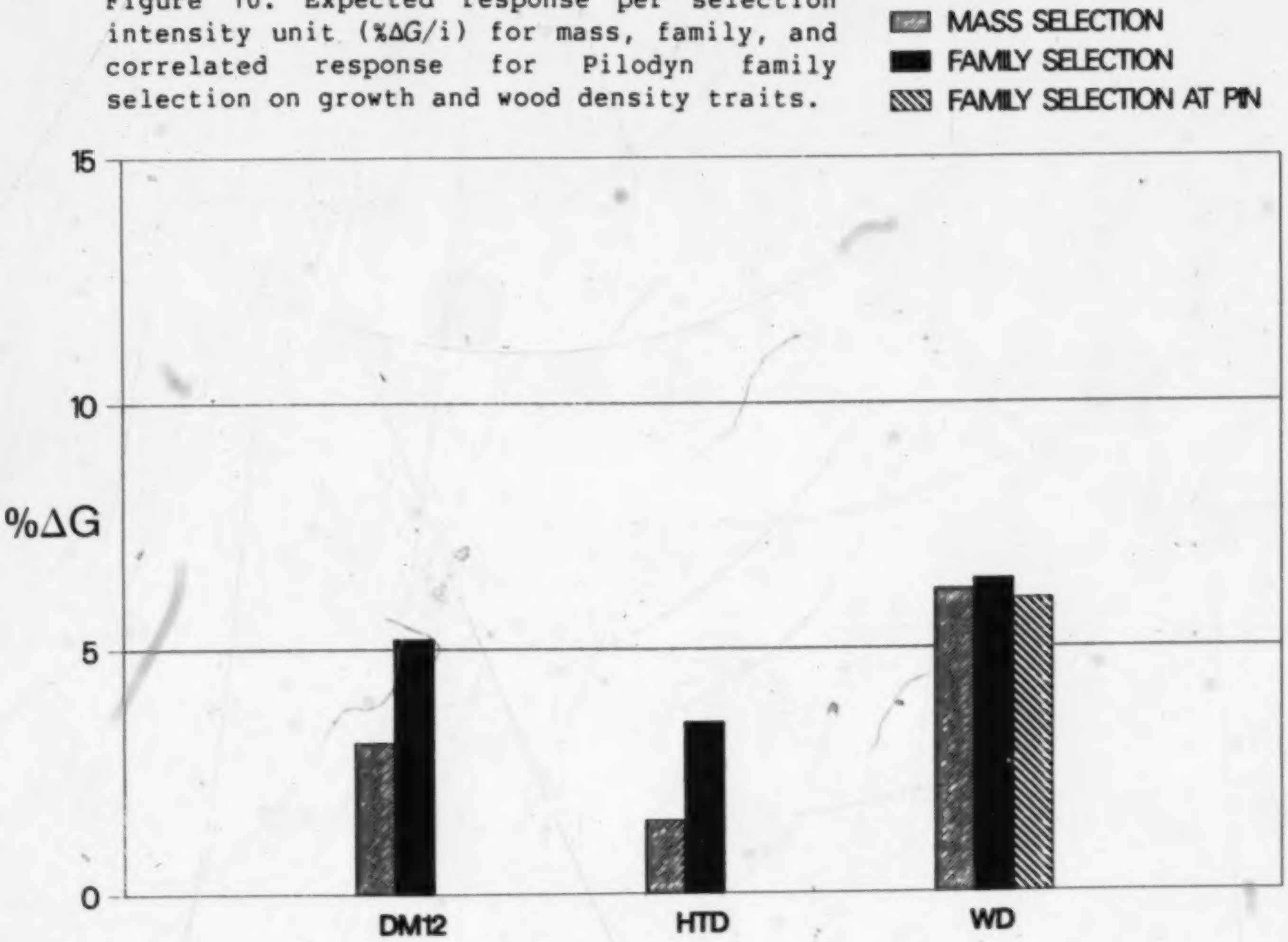
The genetic correlation between the Pilodyn measure (*PIN*) and wood density (*WD*) was high (r_A=-0.95±0.02). Because of the high genetic correlation and heritability, the efficiency of correlated response to family selection was 97% (Fig. 10; Table E5), and it would thus appear from this study that the Pilodyn is a valuable instrument for family selection of wood density in 12½ year old Douglas-fir. Thus family selection may be a useful application of the Pilodyn but it is likely less effective for individual selections as would be practised in the Douglas-fir provenance-progeny tests in France (Bastien *et al.* 1985). It may also be, as Sprague *et al.* (1983) found, that certain types of Pilodyn configurations (e.g., different pin sizes) (and/or spring strength) are more effective than others.

3.3.2 Relationships Between Wood Density and Growth and Form

Unfortunately strong negative genetic correlations exist between wood density and growth traits Table 17. (r_A=-0.53±0.19). A strong negative relationship between growth and mean wood density was also reported in the French Douglas-fir provenance-progeny tests (Bastien *et al.* 1985). They also found a negative genetic correlation of wood mean density vs. wood heterogeneity, but no unfavourable correlations of wood heterogeneity and growth. Such results are discouraging for the simultaneous improvement of growth traits, wood quality, and wood density in Douglas-fir.

Relationships between wood density and form traits are also presented in Table 17. Although the simple correlations between branch number and branch angle were non-significant

Figure 10. Expected response per selection intensity unit (%$\Delta G/i$) for mass, family, and correlated response for Pilodyn family selection on growth and wood density traits.



(P>.05), significant negative genetic correlations exist:

r_A=-.32±.27 (*WD* and *BN*) and r_A=-.41±.27 (*WD* and *BA*),

and environmental correlations are positive (Table 17). Proportional branch thickness (*BTT*) was significantly correlated, r, (P<.001) to wood density and this association also shown by the genetic correlation (r_A=.26±.23; Table 17). Thus selecting for families of high wood density will produce a population of trees with fewer branches, proportionaly thicker branches and more acute-angled branching; this amounts to selecting for the heavy-branching form type. Much of this association may have to do with the strong negative association of growth vs wood density, and the positive association of fine-branching vs growth. Thus a negative association of wood density vs fine-branching is not independent of other key relationships. Negative relationships between wood density and crown form traits have also been reported in Australian radiata pine (Dean *et al.* 1983).

There were significant (P<.001) negative correlations between wood density and stem attribute traits (Table 17). The strongest of these relationships on a genetic basis was that between sinuosity and wood density (r_A=-.28±.22; Table 17), which indicates that by selecting for wood density, smaller and less sinuous trees will be favoured.

TABLE 17. Phenotypic, genetic, and environmental correlations between wood density and growth traits, wood density and crown form traits and wood density and stem attribute traits.

		DM12	*HTD*
WD			
	r	-.46 ***	-.21 ***
	r_A	-.53±.19	-.33±.27
	r_{Pi}	-.41	-.17
	r_{PHS}	-.49	-.28
	r_E	-.60	-.24

……

	BN	*BA*	*BTT*	*BLT*
r	-.00 NS	-.01 NS	.08 ***	.02 NS
r_A	-.32±.27	-.41±.27	.26±.23	.12±.24
r_{Pi}	-.05	-.07	.02	.01
r_{PHS}	-.23	-.37	.25	.10
r_E	.17	2.72	-.46	-.15

……

	SIN	*FORK*	*LAFL*
r	-.13 ***	-.10 ***	-.06 ***
r_A	-.28±.22	.09±.27	-.16±.24
r_{Pi}	-.14	-.10	-.07
r_{PHS}	-.22	-.07	-.14
r_E	.02	-.24	-.00

*, **, ***= significant at .05, .01, .001 levels of probability.

3.3.3 Growth and Wood Density Selections

Simultaneous improvement of wood density and growth characteristics is difficult in this population, because of the antagonistic genetic relationship r_A=-.53±.19 (*WD* and *DM12*). *DM12* was used as the growth characteristic because of its strong association with stem volume and because of its significance levels at site CLES, where wood density measurements were taken. Index coefficients for multiple trait selection of *WD* and *DM12* where both traits are given equal value were:

WD	*DM12*
1.85	1.58

When families were ranked according to their genetic merit for an aggregate breeding value of *WD* and *DM12*, the response (R_{OBS}) for a selection intensity of 1:2 was 10.04 kg/m^3 of *WD* with a concurrent decline of nearly 1 mm in *DM12*.

A plot of the response (R_{OBS}, ΔG) of the traits for a selection intensity of 1:2 in standard deviation units to changing economic weights of *WD* in relation to *DM12* is given in Figure 11. The correlation between the index (I) and its genetic worth (H), r_{HI}, for the changing economic weights ranged from 0.8 to 1.0 and averaged 0.9; thus indicating the relative efficiency of the index *IWD*. The value and efficiencies of index selection are most useful for negative

Figure 11. Response curves (R_{OBS} and ΔG) for wood density and diameter holding the economic weight of diameter at one and changing the weight on wood density, *IWD*.

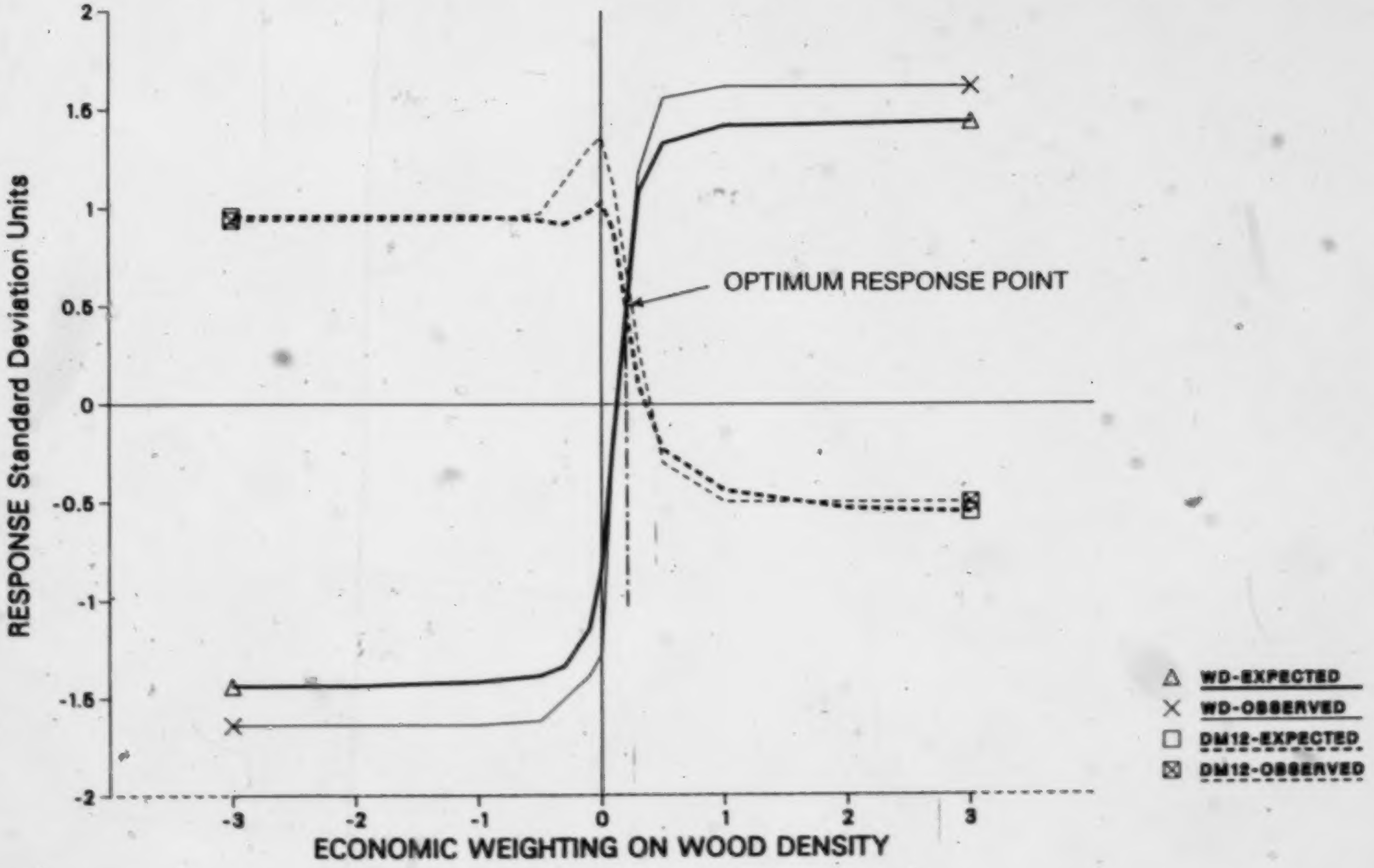
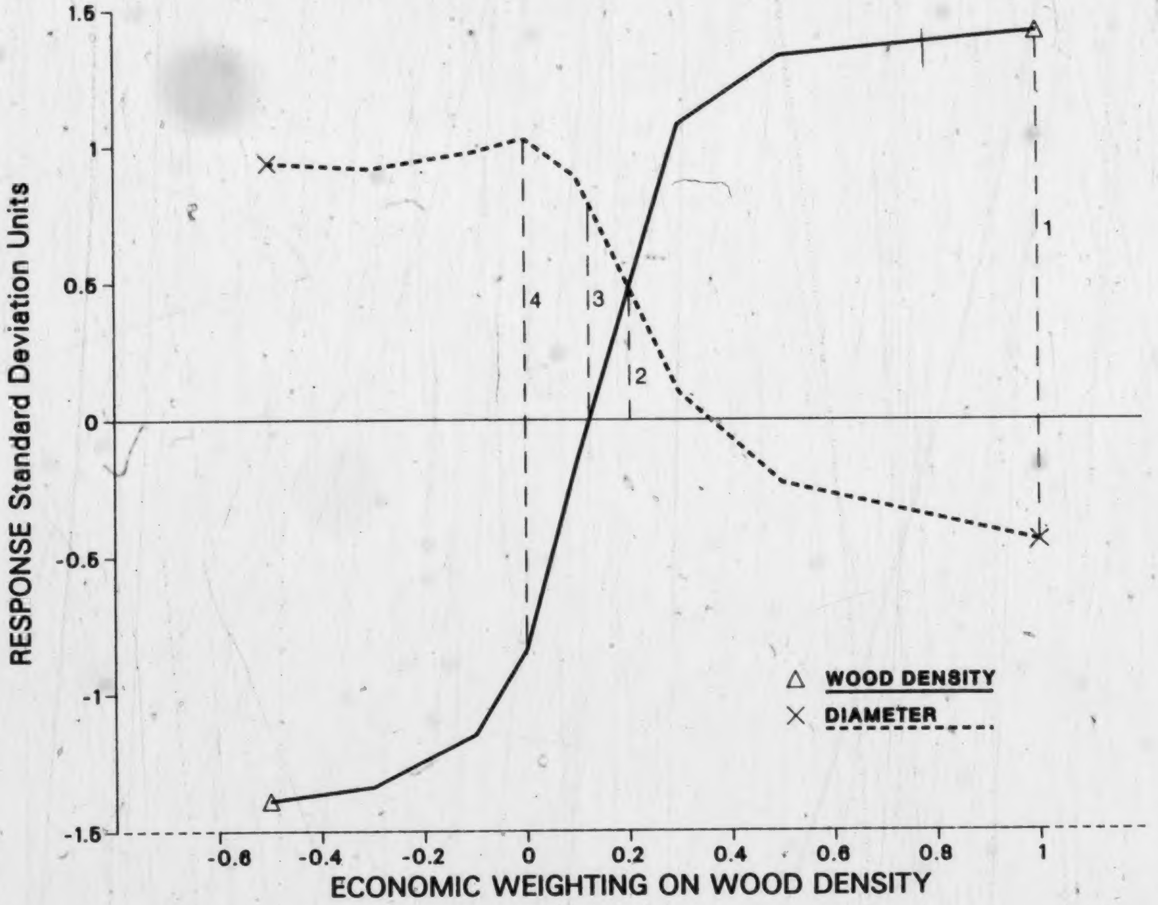


Figure 12. Response curves (ΔG) for wood density and diameter for the selection index *IWD* emphasizing selection strategies.



genetic correlations (Hazel and Lush 1942), where it can elucidate important selection strategies. The appropriate selection strategy depends upon the value that each trait has in the index and the relative certainty we can apply to those values. Four such strategies that might be employed in the improvement of wood density and growth are demonstrated in Figure 12.

1. Option 1: When a unit of wood density is of equal value to a unit of diameter, the overall aggregate value would favour wood density response to diameter response. The assumption of equal values, or any other known value relationship, even if it were known to be true in present market conditions, however, could not be predicted for the future.
2. Option 2: The optimum strategy is one of maximizing the minimum response to selection when values are highly uncertain and subject to unpredictable changes (Namkoong 1979). The optimum point in this selection strategy is at the curve intersection point. Neither trait is maximized at this point; indeed because of the strong negative genetic relationships between these two traits the maximin point achieves only 42% of the maximum response (R_{OBS}) to *DM12* and 72% of the maximum response (R_{OBS}) to *WD*. However, this point is the maximum/minimum (maximin) response point for both traits and is the most appropriate if we believe both traits are economically valuable, but there is high uncertainty as to their

value functions. By selecting for positive response in both traits at this point the selection process can begin to break the negative correlation between these traits.

3. Option 3: This option constrains the change in wood density by using a restricted index as per Kempthorne and Nordskog (1959). This strategy is also a conservative strategy. It makes no assumptions as to the intrinsic value of wood density and assumes there is enough uncertainty as to its value that we should be unwilling to let it decline.
4. Option 4: This assumes that the decline in wood density by selecting for diameter is slight and economically acceptable. Although heritabilities for wood density have been reported as being high, the variability available for selection is low (Bastien *et al.* 1985). The coefficient of variation of stem volume for half-sib means is three times that for wood density. Therefore, the indirect losses in *WD* by the selection of stem volume (through *DM12* in this case) may be comparatively low compared to gains in volume even accounting for the high heritability of *WD*. At a direct selection for *DM12* on its own, with a 1:2 selection intensity, wood density declines by 0.5 (R_{OBS}) of a standard deviation (6.25 kg/m^3) or by 1.75% of its mean. This strategy would ignore wood density under the assumption that a slight decline in wood density in the population may have

little or no economic impact on the resource.

Before selection decisions and strategies are made, however, certain facts need to be known about wood density and its estimation. Information of a practical nature should address the following points regarding wood density:

1. Is juvenile core wood density of any practical consequence to the value of the mature stem wood density and clear wood product?
2. Are selections for wood density worth comparative gains for wood heterogeneity (Bastien *et al*. 1985) and losses in form?

We need to have information of this nature to ensure wood density has an intrinsic value. If it does have an intrinsic value options 3 and especially 2 are the best choices and it should have high emphasis in mass selection phases of multi-stage selection; e.g., plus tree selections and within-family selections. Phenotypic selection for wood density will be highly efficient compared to growth and form selections.

3.3.4 Wood Density Summary

1. Heritabilities for wood density were high (h^2_i =0.90±0.28) - wood density is a trait that can be effectively improved through mass selection.

2. Unlike the results of Bastien *et al*., the Pilodyn proved very effective. With a genetic correlation of -0.95 the efficiency of using the correlated response to family

selection was 97%.

3. Correlations with growth traits were strongly negative.

4. Correlations with form traits reflect this negative relationship with growth and were also unfavourable.

5. An antagonistic relationship between wood density and heterogeneity of wood density (Bastien *et al.* 1985) is also of concern considering the importance of a uniform product (Zobel *et al.* 1982).

6. Index selection is highly effective for selections involving negative correlations and can be used to minimize the impact of the negative relationship between wood density and growth. Several selection strategies were examined. When the unfavourable correlations with wood heterogeneity and form are ignored, options that constrain the loss in wood density -3- or seek to maximize the minimum expected response to both traits -2- are best.

4. DISCUSSION

4.1 Expression of Genetic Differences

Twenty of the twenty-one traits of growth, form, and wood quality investigated in this study had significant amounts of additive genetic variance from which to base selections. Non-additive genetic variance, σ^2_D, was not significant for most of the traits, except for branch angle, bole taper, and lammas incidence; but even in these cases was much less than the additive genetic variance. G.E.I. interaction, as (determined by σ^2_{sf}) was non-significant for all traits. A site×cross source of information (σ^2_{smf}) was significant for the two later height measures (*HT10*, *HT12*), but was not significant for any other traits.

4.1.1 Selection Parameters for Individual Traits

With additive genetic variance being the major significant source of genetic variance available, selection for additive genetic effects and the creation of random mating populations within seed orchards is likely to remain the major vehicle of tree improvement for the coastal Douglas-fir program in British Columbia. In this selection process heritability is important as a method of determining the predictability of response to selection. Heritability is also important in determining the appropriate selection procedures: i) for high heritability traits where the phenotype expresses the genotype - mass selection can be emphasized, ii) for low to moderate individual tree heritabilities - progeny test selection should be emphasized. Two other parts in determining the response to selection are: i) the selection intensity applied and ii) the phenotypic variance (or standard deviation). Thus predicted response to selection will depend upon the degree of the inheritance of the trait, the amount of variability that can be selected upon, and the intensity of selection.

Heritabilities (which express the selection genetic variances over phenotypic variances), coefficients of variation (which express the amount of variation in the population in relation to their means as a percentage), and percentages expected gain per selection intensity unit are summarized for all twenty-one traits in Table 18.

Only two traits, branch angle (*BA*) and wood density (*WD*), demonstrate high individual tree heritability ($h_i^2 \geq 0.50$) values (Table 18). High individual tree heritabilities for branch angle and wood density have also been reported in other Douglas-fir studies. Phenotypic selections, therefore, can be effective for improving these traits in Douglas-fir.

Traits that demonstrate moderate genetic control ($h_i^2 \geq 0.15$; $h_f^2 \geq 0.7$) are: early height (*HT06*), diameters (*DM06*, *DM10*, *DM12*), branch number (*BN*), proportional branch thickness (*BTT*), proportional branch length (*BLT*), and sinuosity (*SIN*). For these traits, gains of 5-10% per unit of selection intensity for family selection and 2-5% per

TABLE 18. Summary of selection parameters for all traits.

Trait		Mass selection			Progeny test selection		
		h_i^2	CV_{Pi}	$\%\Delta G_i/i$	h_f^2	CV_{PHS}	$\%\Delta G_f/i$
Growth							
HT06	height 6th growing season	0.14±0.06	28.00	3.86	0.73±0.31	6.10	8.87
HT10	height 10th growing season	0.12±0.04	22.36	2.68	0.64±0.23	4.85	6.19
HT12	height 12th growing season	0.14±0.05	17.12	2.40	0.66±0.23	3.96	5.18
HTD	growth from 10th to 12th year	0.08±0.05	18.12	1.45	0.59±0.33	3.34	3.93
DM06	diameter 6th growing season	0.19±0.07	28.84	5.48	0.77±0.28	7.18	11.00
DM10	diameter 10th growing season	0.16±0.06	24.72	3.96	0.75±0.26	5.73	8.55
DM12	diameter 12th growing season	0.16±0.06	16.94	2.79	0.73±0.25	4.03	5.85
VOLM	volume measurement	0.10±0.05	44.76	4.26	0.55±0.29	9.32	10.25
Form							
BN	branch number	0.19±0.07	21.76	4.10	0.82±0.30	5.21	8.56
BA	branch angle	0.73±0.24	10.61	7.72	0.92±0.30	4.73	8.66
BT	branch thickness	non-significant					
BTT	branch/stem diameter ratio	0.26±0.10	11.64	3.04	0.78±0.31	3.36	5.27
BL	branch length	0.11±0.06	15.64	1.68	0.52±0.27	3.56	3.68
BLT	branch length/total height 10	0.19±0.07	11.80	2.22	0.77±0.30	2.93	4.48
KI	knottiness index	0.16±0.07	21.82	3.38	0.69±0.32	5.16	7.15
TAPER	taper measurement	0.10±0.05	25.70	2.53	0.57±0.30	5.35	6.04
SIN	stem sinuosity score	0.26±0.09	34.41	8.97	0.86±0.30	9.45	16.34
FORK	forking score	0.08±0.03	19.06	1.49	0.66±0.27	3.28	4.33
LAFL	lammas score	0.10±0.05	15.47	1.60	0.61±0.28	3.19	3.88
Wood Quality							
WD	wood density (5mm cores)	0.90±0.28	6.97	6.23	0.93±0.30	3.41	6.37
PIN	Pilodyn pin penetration	0.81±0.26	12.06	9.71	0.90±0.29	5.72	10.23

unit of selection intensity for mass selection appear achievable (Table 18).

Traits that demonstrate low genetic control ($h_i^2 \approx 0.1$; $h_f^2 \approx 0.5$) are: later height measurements (*HT10, HT12*), stem volume (*VOLM*), branch thickness (*BT*), branch length (*BL*), stem taper (*TAPER*), forking (*FORK*), and lammas occurrence (*LAFL*). The low individual tree (h_i^2) and moderate family (h_f^2) heritabilities for these traits indicates that family selection will more effective than mass selection. Gains of up to 5% can be expected for this type of selection. For traits where large amounts of phenotypic variability is available among families, such as volume (*VOLM*), substantial improvement can be made for progeny test selection (≈10% per selection intensity unit) even though individual tree heritabilities are low (Table 18).

4.1.2 Relationships Between Traits

The important parameters between traits are genetic and phenotypic covariances and correlations; correlations among the traits of growth, form, and wood quality are summarized in Table 19. Genetic correlations were classified as negligible $r_A<0.15$ (0), weak $r_A=0.15-0.29$ (+, or -), moderate $r_A=0.30-0.44$ (++, or --), or strong $r_A \geq 0.45$ (+++, or ---). The direction and significance levels of phenotypic relationships are given below the diagonal (Table 19).

The major significant relationships that affect selection for improvement in areas of growth, form, and wood

TABLE 19. Summary of genetic and simple phenotypic correlations.

Traits	*HT06*	*HT12*	*DM12*	*VOLM*	*BN*	*BA*	*BT*	*BTT*	*BL*	*BLT*	*TAPER*	*SIN*	*FORK*	*WD*
HT06		+++	+++	+++										
HT12	+++		+++	+++	+	0	0	--	++	---	--	++	-	---
DM12	+++	+++		+++	+++	+	+	---	+	+	+	0	0	---
VOLM	+++	+++	+++		+++	+	+	---	+	-	+			---
BN		+	0	+		+	+	---	+	0	+++			--
BA		---	---	---	+++		0	-	0	0	0			--
BT		+++	+++	+++	0	---		++	++	0	+++			
BTT		---	---	---	--	0	+++		0	0	+			+
BL		+++	+++	+++	0	---	+++	---		+++	0			
BLT		---	--	---	---	---	+++	+++	+++		0			0
TAPER		---	+	0	+	---	+++	+++	0	+++				0
SIN		+++	+++											-
FORK		-	++											0
WD		---	---	---	0	0	---	+++	---	0	0	---	---	

Below diagonal: simple phenotypic correlations

r=0; P>.05

r=+,-; 0.01<P<0.05

r=++,--; 0.001<P<0.01

r=+++,---; P<0.001

Above diagonal: genetic correlations

r_A<0.15 (0, negligible);

r_A=0.15-0.29 (+, or -, weak);

r_A=0.30-0.44 (++, or --, moderate);

r_A≥0.45 (+++, or ---, strong).

quality are the strong negative relationship between growth traits and wood quality (wood density) and the weak to moderate, positive relationships between stem biomass and a form complex of profuse, light, and excurrent branches. (fine-branching form type).

Other relationships that exist are moderate, positive correlations between height and sinuosity (r_A=0.41) - a similar negative relationship was found by Jarret (1978) in French Douglas-fir -, moderate negative correlations between height and taper (r_A=-0.38), weaker but positive correlations between diameter and taper (r_A=0.15), and strong positive genetic correlations between branch number and taper (r_A=0.57), and branch thickness and taper (r_A=0.73).

Genetic relationships between wood density and crown form traits reflect the strong, negative correlation that exists between growth traits and wood density. These include a moderate, negative genetic correlation between branch number and wood density (r_A=-0.32), and between branch angle and wood density (r_A=-0.41); and a weak positive association between wood density and proportional branch thickness (r_A=0.26).

4.1.3 Selection of Traits

Early height growth can be used as an indicator of establishment and early vigour, but also where early selections are necessary it provides good strong positive correlations with later juvenile height, diameter and volume traits (Table 19, Fig. 6). Selections for yield (stem volume) were most efficiently made by using a diameter measure rather than total height. A multiple trait index using the the genetic covariances of height at age 6, height at age 12, and diameter at age 12 to predict the ranking of progeny families for stem volume; could only marginally improved the ranking (r_s=.99) compared to ranking that occurred using indirect selection for stem diameter (r_s=.89). Height selections were not nearly as good for successful predictions of progeny families for stem volume (r_s=.55). This reflects the stronger genetic correlation between *DM12* and *VOLM*. Velling and Tigerstedt (1982) found that diameter had significant genetic covariances with harvest index (*HI*) - a ratio of stem-wood fresh weight to total tree (branches and stem) fresh weight - compared to a non-significant genetic covariance between height and harvest index. Diameter measurements also maintain higher heritabilities (Table 18), therefore selections that are aimed at increasing yield and biomass in Douglas-fir should use diameter rather than total height.

The growth related traits of later height measurements, branch thickness, and branch length, showed poor expression of genetic differences - especially on individual sites and at the Lake Cowichan site (CLES). This was demonstrated by a lack of significance for sources of variation for additive genetic variances (σ_t^2), high standard errors for additive genetic variance, and low individual tree heritabilities especially on the individual site analyses. Insensitivities of the plantation sites, especially large row plots (nine trees) with relatively few replications (three reps) on an undulating site of coarse-textured soils accounted for part of this error. This was manifested by increases of σ_w^2, which is the major part of the error variance for genetic sources of variation (σ_f^2).

Biological reasons can also be cited for this poor discrimination of genetic differences in growth traits. Young seedlings in their first years of growth are affected mainly by microsite influences; the major source of variation is expressed on a tree-to-tree level and inherent growth rate differences can be expressed if there is adequate replication. As trees grow into crown canopy, microsite influences decline and the accumulation of large-scale environmental effects becomes more influential; trees start to grow as a stand and the stand-to-stand level of variation is most strongly expressed. Simmonds (1978) pointed out that the potential biomass of a crop is eventually determined by the sum total of its local environment. Inherent differences in growth rate potential can be limited by this environmental ceiling. As trees enter the second growth phase with the onset of intraspecific competition, the environment becomes more limiting for the expression of inherent differences. Full utilization of inherent growth rate potential will require stand management techniques such as thinning. Rather than attempt high gains through strong selection pressures for yield, low intensity selection for the culling of poor preformers would be better practiced.

Quality traits that are not a direct reflection of growth, such as branch angle, branch number and wood density; and growth traits when expressed in terms of partitioning of biomass (e.g. branch thickness/ stem diameter, branch length/ total height) express genetic differences more strongly (Table 18). These results reflect very closely the observations made on Scots pine by Velling and Tigerstedt (1984). Simmonds (1978) stated in relation to tree breeding that "...the first objective is simply the adapted ecotype which can realize the biomass-potential of the local environment; but in addition, the tree breeder may have some opportunity to exploit the potential of his species for improved partition (between stem and branch) and wood quality (straightness and density).".

Selection of quality and form traits can be effective and should concentrate on the promotion of the pleiotropic action for the formation of a fine-branching tree. Campbell (1963) demonstrated significant positive phenotypic correlations between thick and acute-angled branches and between fewer branch numbers per whorl and thicker branches. These relationships were found to hold for this study, especially in the partial correlations that control for the effect of stem volume. Moderate genetic associations between branch number and stem diameter, and between branch number, proportional branch thickness and stem diameter, offer a way in which the pleiotropic action of genes might be used to not only improve stem yield but also to promote a finer branching form type over a coarse branching form type. By actively selecting for the finer branching form type, although more branches per whorl would be promoted, there would be concurrent declines in proportional branch thickness (*BTT*) and proportional crown width (*BLT*), and increases in stem diameter (*DM12*) and branch angle (*BA*). Some of these relationships were also apparent in Jarret's (1978) study, especially between yield (height) and branch angle (r_A=0.96), and also between branch angle and branch number (r_A=0.52). They were also shown in Scot's pine by Velling and Tigerstedt (1984), who used the same partitioning traits and came to the same conclusions regarding the promotion of the finer branching form type. Karki (1983) has claimed that these form types in Finnish Scot's pine and Norway spruce might be controlled by single-gene action. This is not at all apparent in Douglas-fir, but the close similarity of the results in this study to those of Velling and Tigerstedt's (1978) and Merrill and Mohn's (1985) in white spruce, suggests that form and yield can be manipulated through the pleiotropic action of additive genes in conifers. Index selection of key form and yield traits can use genetic covariances to encourage the formation of this form type. Using a composite trait such a knottiness index (a ratio of branch wood cross-sectional area to stem wood area) can also improve form, but does not improve the correlation for the fine-branching form type.

Selection for stem form traits of sinuosity and forking offers similar results to other studies. High within-family variance component percentages for these traits ($\sigma_w^2 \geq 80\%$) indicates that much of the variation is uncontrollable and phenotypic selections are unlikely to be useful. Sinuosity is under moderate genetic control and should respond well to family selection (see: Jarret 1978; Birot and Christophe 1983; Adams and Howe 1985). A moderate positive genetic correlation beteen height and sinuosity was also shown by Jarret 1978. Thus selections made on the basis of height will promote sinuosity in young plantations. Diameter did not show this positive correlation. Forking and ramicorn branching had low heritabilities. Family differences were non-significant for forking in the French tests (Jarret 1978; Birot and Christophe 1983), and was also reported as having a low heritability in Australian tests of radiata pine (Cotteril and Zed 1980). Although individual tree heritabilities are low for these traits the large phenotypic variances between families and moderate family heritabilities suggest that family selection can be used for improvement for these traits.

Phenotypic selections for wood density should be very effective for both first generation mass selections or within family selections in progeny tests. The Pilodyn proved to be a very effective way of making selections for wood density in this study. This was indicated not only by a high heritability for this method of estimating wood density but also by a strong genetic correlation between the Pilodyn values and increment core estimations. Relative efficiency for family selection of wood density using the Pilodyn was 97% (Fig. 10). Bastien *et al.* (1985) did not find the Pilodyn to be as effective, but results can vary because of pin size, spring strength (Sprague *et al.* 1983).

Although selections for growth and form can utilize positive genetic associations to benefit both traits, selections of wood density and traits of yield must contend with a strong negative correlation. A strong negative genetic correlation between wood density and yield traits has also been reported in other Douglas-fir populations (Bastien *et al.* 1985). Index selection can be most valuable for the genetic improvement of negatively correlated traits (Hazel and Lush 1942). It allows an empirical choice of selection options that can be made based on expected gains of each trait in the index. Choices for the wood density and diameter index *IWD* can be made from four possible selection options:

1. The first option assumes that each trait has an equal economic weight; selections for aggregate breeding value based of this assumption will favour selection for *WD* over *DM12* because of the higher heritability of *WD*. This

assumption of equal economic weight implies that these economic weights are known and are likely to be maintained for the rotation age of Douglas-fir.

2. The second option is to maximize the minimum expected gain for the simultaneous improvement of both traits (the curve intersection points). This option is most appropriate when the economic weights to the traits are highly uncertain, unpredictable, and likely to change, but both traits are valuable - this is the most realistic scenario for wood density and yield in Douglas-fir. This is also the most conservative strategy as no attempt is made to set explicit values. It is also the best strategy to break the negative correlation by selecting genotypes that display breeding values above the average for both traits, thus begining the process of breaking down this negative correlation.
3. The third option places a restriction on wood density as per Kempthorne and Nordskog (1959). This option seeks to place as much emphasis as possible on yield yet restrict the losses that might occur in wood density. This is less conservative than the second option, yet seeks to maintain wood density at present levels. The assumption here is that wood density has no intrinsic value on its own and is not worth selecting for, yet there is enough uncertainty as to the value if it should decline that we are unwilling to maximize yield response.
4. Option four is based on the idea that a slight loss in

wood density is unlikely to have any serious impact on the resource. Heritability of wood density is the highest of any of the traits reported in this study yet the phenotypic variability is the lowest.

With only the information here and a knowledge that wood density has an intrinsic value (Kellog 1982), the second option is the safest and most conservative strategy to apply. However with the report of Bastien *et al.* (1985) of positive genetic correlations between wood density and wood heterogeneity and the apparent value of wood homogeneity (Zobel *et al.* 1982), large question marks still remain.

4.2 Measurement Strategies in Douglas-fir

One important objective of this study was to establish key indicator traits that can be useful for the assessment of growth, form, and wood quality in juvenile Douglas-fir progeny tests. The criteria for choosing key indicator traits were the effectiveness of selecting for the traits as determined by their selection parameters (h^2, *CV*, and %ΔG; Table 18), and for their relationships to other key traits as determined by their correlations (Table 19). In addition, experience derived from this study with respect to the methodology of measuring traits can be used to establish guidelines for the assessment of traits of growth, form, and wood quality in Douglas-fir progeny. Other valuable references that should be consulted are the works of Jarret (1978), DeChamps (1978) and Adams and Howe (1984) in

Douglas-fir; and some of the Finnish work with Scots Pine (e.g. Velling and Tigerstedt 1985).

4.2.1 Growth Traits

Height and diameter are the key traits of growth and yield. Although height alone is not a good trait for predicting stem biomass, it indicates establishment and survival potential especially at the early stages of growth for Douglas-fir. Stem biomass is best predicted by a diameter measure. Diameters of juvenile Douglas-fir can be taken, adequately and quickly with calipers, at a reference height as established by Kovats (1977). In plantations over 5 to 6 m tall, diameters can be taken from the breast high (1.3 m) stem segment at a mid-point average of the stem segment. In plantations, where breast high measurements are not feasible (plantation average < 5 m) diameters can be taken at a stem segment section that is clearly expressed throughout the plantation. In this study diameter measurements were taken at stem segment seven (Fig. 5), and this was usually equivalent to a breast high measurement.

4.2.2 Form Traits

The key traits that should be emphasized for crown form are branch number, branch thickness and branch angle. Branch length need not be measured due to the strong positive correlation with branch thickness. Once a stem segment has been chosen from which to make the diameter measurements, crown form measurements can be taken in the whorls directly above and below the stem segment (Fig. 5).

Because branch number is difficult to assess, especially when trying to determine the difference between primary and secondary branching (see also Campbell 1963, Jarret 1978), a subjective measure of branching that totals all branches from the whorl to the first area of clear stem wood below the whorl (5-7cm) should be made. Small secondary branches can be added up to make equivalents of primary branches (e.g., 4×10mm secondary branches ≈ 1×20mm primary branch).

A single measure, for each of the branch thickness and branch angle measures, should be taken at each of the whorls. In this study two randomly chosen branches were measured at each whorl. However, the experience gained from the study suggests that a single, subjectively chosen branch that reflects the average at each whorl is a more efficient measuring technique. Many form characters may best be assessed on a subjective basis, but if they are given a metric measurement based on a subjective judgement (e.g., the branch that most reflects the average at the whorl) rather than a categorical value, it is easier for data manipulation and interpretation.

Form traits can be assessed on a simple scoring method (see **2.3.4**) or through various measuring and scoring methods as reviewed by Jarret (1978), or outlined by Adams and Howe (1985). One can also treat these traits as threshold traits

(Falconer 1982) with a dichotomous distribution (e.g., scoring class-0, 1 & 2 =0; scoring class-3, 4 & 5=1) or use a polychotomous threshold distribution. Besides the advantage of overcoming problems of scale, measuring stem and upper crown traits as threshold traits is easier since only damaging incidences need to be recorded and time wasting evaluations are eliminated.

Determining lammas incidence and damage in older trees, as was done in this study, is a time consuming process. Lammas incidences should be measured in the 6 to 8 year class and not on trees any older than 10 to 12 years.

4.2.3 Wood Quality Traits

Juvenile wood quality assessments may best be made in trees older than those of this study, preferably at 15 years or older (see 1.4.1, Kellogg pers. comm.). The Pilodyn proved to be a very effective instrument for wood density selections. Although some Pilodyn configurations have proven less reliable (Sprague *et al*. 1983, Bastien *et al*. 1985) the one used here with a 2.5 mm pin diameter and a 6 joule spring appeared very useful.

4.2.4 Timing of Measurements

Measurements for the assessment of juvenile growth, form, and wood quality in Douglas-fir can be scheduled as follows:

1. Age 6-8 - height and lammas incidence plus other

measurements of survival and establishment.

2. Age 12-15 - diameter, branch number, branch thickness, branch angle, threshold measurements of stem sinuosity and forking, Pilodyn measurements (Fig. 12).
3. Age 15-20 - after a thinning operation, sub-sampling for wood heterogeneity and more details of partitioning and form types to see if they can be tied into the concept of harvest index.

4.3 Improvement Strategies for Douglas-fir

The progress of tree improvement is through both selection and breeding. This study has emphasized selection; however the two procedures cannot be treated independently, and selection strategies depend on breeding strategies.

Breeding with a high value conifer, such as Douglas-fir, grown in north-temperate latitudes, such as British Columbia, will require breeding strategies that reflect conditions of:

1. long economic rotation times (80 years minimum),
2. natural populations that are already well adapted to the local environment,
3. a large and variable land base that necessitates extensive rather than intensive silvicultural management.

The selection process should be utilized to be most efficient at different levels of selection within the breeding program. Phenotypic selections of high heritability traits, such as branch angle and wood density, can be emphasized in selections of recombinants within families. Index selection using family information, as in the progeny testing here, will be emphasized when selecting for high levels of GCA.

4.3.1 Breeding Strategy

The breeding design used in this study, the NC II tester design, was ideal for the stated objectives of this study; and selection from this experiment has emphasized progeny test selection using the genetic relationships between a parent and its half-sib progeny for the selection of parents. The selection strategies outlined here are thus easily transported to progeny test selection where GCA is estimated from open-pollinated families. However one of the major objectives of most breeding programs is to produce a population for the next generation of selection. A first generation progeny test selection scheme as outlined in this study does not achieve this objective, and recombinants of the select trees have yet to be produced for further breeding.

In fast growing species, parents can be tested, many recombinants can be generated through single-pair matings of proven parents, high selection intensities can be practised on these recombinants, and even the selected recombinants can be O.P. progeny tested (Cotterill 1984). This can be done very effectively in the short rotation of radiata pine in Australia, for instance, where decisions on progeny tests can be made between 4½ to 7½ years (Cotterill 1984). Fast generation breeding options are less attractive to Douglas-fir improvement. There is no all around "best option" for breeding of Douglas-fir, and it as often as not depends upon the resources and commitment made by the agencies involved. Because breeding options are reduced in north-temperate conifers it is most important that efficiencies in the selection process be maximized. Examples of how these efficiencies can be made for two of the most common breeding plans for Douglas-fir are given here:

1. The first generation of breeding in Douglas-fir often combines the objective of testing the first generation of selection together with producing second generation material (as has been done in B.C. with a half-diallel program); second generation selections can be made, but a loss is made in the potential selection intensities that can be applied to second generation stock - the recombinants - for the cost of testing poor first generation material. Planting designs for this breeding plan must be both efficient for testing and ranking families but also for emphasizing genetic differences among individuals within families, selection in family plots will be important. Selections of this recombinant material is also reliant on the phenotype to express the genotype. The low individual-tree heritabilities for many of the traits has emphasized that genotypic

selections are more important in tree improvement of Douglas-fir than phenotypic selections. The most efficient selection strategy for a single trait or index will involve the use of a combined index that uses family and individual information to make second generation selections. Cotterill (1986) found this breeding/selection strategy to be the most efficient per generation/decade of ten strategies investigated for traits of low to moderate (.05-.40) heritabilities. A multi-stage family/within family can be used effectively when high heritability traits are used in the second stage. An example of this multi-stage selection can: 1) emphasize diameter (yield) and fine branching (*BN* and *BT*) in a low intensity family selection and 2) emphasize branch angle (*BA*) (for its correlation with fine-branching) and/or wood density (*WD*) in a within-family selection. The major difficulty with the half-diallel are the limitations on the parents that can be effectively handled, and the manpower and effort that is needed to make all the appropriate crosses.

2. A cheaper and efficient first step to screen parents for GCA are open-pollinated progeny tests. Planting design here should be efficient for family selection only, therefore should seek to minimize the error variances with corrrect blocking, and many replications of small or contiguous plots. Where parents have been cloned recurrent selection can use the methods and traits

established in the progeny-test selection schemes developed in this study. Recombinants from selected parents can most effectively be regenerated from single-pair matings. As selections from the next generation will rely only on within family selections; traits should be chosen that exhibit moderate to high individual tree heritabilities, and planting design should emphasize efficiencies gained by high selection intensities in large family plots. Because this will be an inefficient selection process, it may be wise to terminate this test after selection for early height growth (≈*HT06*) and/or a trait such as branch angle (*BA*) and/or lammas incidence (*LAFL*) (if this trait is to be considered selection should be at this stage). This selection process is inefficient also for the use of generations but by using the appropriate selection strategies, (i.e. choosing the most effective traits) and by physically lifting the selected material for second generation breeding not that much time needs to be lost.

4.3.2 Planting Design

Inefficiencies of the experimental layout used in this study have been demonstrated by the lack of precision and inability to detect significant differences for growth traits on the individual sites. Three basic principles are used to control or minimize experimental error, these are:

replication, randomization, and local control or blocking. Although local control can be a problem on forest sites it was less of a problem as demonstrated by the error variances (σ^2_{rmf}) than lack of replication and randomization that was caused by too large a plot on too few replications. The statistical efficiency of the test would increase if there was a reduction in the within-plot error variance (σ^2_w). This is especially noticable at CLES where the plots are row plots that run up and down a rise on a coarse textured and freely draining soil. The efficiency of allocating trees to reps and plots can be derived (Yeh and Rasmussen 1985) but it depends on what level of selection is being applied.

In the progeny test function, as used in this study, efficiency is maximized by planting seedlings in many replications of small or contiguous plots. This would not be the case however if individuals within families were to be the selection unit. In this case family plots are desirable for efficient discrimination of individuals within families. A planting design that has more reps and fewer trees per plot would be more efficient however. Correct blocking of the experiment to control for environmental heterogeneity is also desirable, especially where relatively few reps are used as in this study. An effort to reduce the environmental variance within plots by having them run with the environmental gradient, rather than across, is especially necessary if within family selection is being practised.

4.3.3 Genotype by Environment Interaction and Adaptation

Sources of variation for additive genetic variance by environment interaction were non-significant for all of the traits investigated in this study. Although limited by only two sites that were not extremely different, there is strong evidence that Douglas-fir is relatively robust in its genotypic stability for these 21 traits of growth, form, and wood quality. For ranking and selection purposes it may only be necessary to test families across 2 to 4 sites. Further plantations on more extreme environments could be established to provide information specifically about genotype by environment interactions.

One of the current controversies in tree improvement work in Douglas-fir is that tight adaptation to narrow ecological zones has been demonstrated in seedling studies (Campbell and Sorenson 1978; Campbell 1979), and indeed one of the criticisms of the B.C. program has been that seed zones are too widely defined (Yeh *et al.* 1981). However there is little evidence from this study, from the recent provenance research in the Pacific Northwest (White and Ching 1985), and in B.C. (Ying pers. comm.) that this tight adaptation carries much beyond the seedling stage. Usually seed sources that do particularly poorly - are ill adapted - are planted on off-site locations (e.g. the southern Oregon source, White and Ching 1985; or low elevation sources planted on high elevation sites, Ying 1984).

Thus splitting the breeding region of Douglas-fir from low to mid-elevation sites of coastal B.C., into multiple breeding units to exploit adaptational differences for increased gain (Namkoong 1984), does not appear warranted. Although it may be considered as an option for channeling selection opportunities for traits (high *WD* populations) and for gene conservation (Namkoong 1984).

4.4 Summary and Future Considerations

This study has emphasized the selection process in the improvement of the Douglas-fir resource for traits of growth, form and wood quality. It has high-lighted key traits, and key associations; that may be effectively measured and selected for:

1. early height can be a useful trait for early establishment and vigour as well as for its use for early selections for growth and yield traits,
2. diameter is the best indicator for yield and biomass,
3. partitioning traits are better indicators of crown quality traits and can be more effectively selected for,
4. genetic covariances among crown form traits can be utilized for selection for a fine-branching form type,
5. selection against sinuosity should be effective and selection for diameter is less likely to promote sinuosity than selections for height growth,
6. selections against forking and lammas growth will be less effective than those against sinuosity,

7. selections of wood density by either increment cores or the Pilodyn will be very effective,
8. there are strong negative correlations between wood density and growth traits and negative correlations between wood density and form,
9. these results are corroborative of similar results in Douglas-fir from France (Jarret 1978, Birot and Christophe 1983), Scot's pine in Finland (Velling and Tigerstadt 1982), white spruce in the Lake States (Merrill and Mohn 1985), and radiata pine in Australia (Dean *et al.* 1983).

The study has also high-lighted key multiple trait strategies and options:

1. selections for growth traits should use family information and not be aimed at achieving high selection intensities and gains but rather the culling of poor genotypes and promotion of good vigourous growers,
2. multiple trait selection for a complex of light, flat branches, and high yield trees should be encouraged in family, combined, and even individual selection using the high heritability of branch angle.
3. several options were investigated for how to handle the negative correlation between growth and wood density; if wood density has an intrinsic value, and it is not adversely correlated with wood heterogeneity (Bastien *et al.* 1985) then selections that maximize the minimum expected response to selection for both traits would

appear to be the best strategy (maximin option two Fig. 12). This would also go some of the way to breaking down this unfavourable correlation. The next best option under these circumstances is to constrain the loss of *WD* - option three (Fig. 12).

4. options for incorporating these selection strategies into current breeding strategies were briefly investigated.

4.4.1 Future Considerations

This study has addressed topics related to the selection of traits of growth, form, and wood quality in Douglas-fir and continues the excellent work in this subject done by Campbell and Jarret. There are many important areas of future research that should be done to extend this knowledge.

Although this study could not identify significant site × genotype interactions it is hoped another study directed at investigating the genetic stability over a more extreme range of sites will more adequately investigate questions related to this.

The experimental material used here should be maintained in order that the expression of the variances and covariances observed here can be tracked over time and clear ideas can be established as to valid ages at which these traits might be evaluated. Early progeny evaluations are essential to the effectiveness of tree-improvement strategies for Douglas-fir.

Detailed wood quality assessments need to be carried out to see if the negative correlations between mean wood density and wood heterogeneity established in France are true of most populations of Douglas-fir. This information is necessary before wood density is actively incorporated as a valuable trait in the selection process and can be found when this progeny test is thinned. Traits relating to harvest index (*HI*, Velling and Tigerstedt 1982) and the detailed relationships among crown form traits may also be more fully investigated at this time.

Research will soon be needed to investigate questions related to advanced generation breeding and selection, for example the effects of mild inbreeding, sublining, and gene conservation. An active research program is necessary if we are to maintain Douglas-fir as a valued resource.

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APPENDIX A: Selection intensity expressed in standard deviations for a population of 22 parent trees

No. Selected	Percentage	Value
1	4.5%	1.91
2	9.1	1.69
3	13.6	1.52
4	18.2	1.39
5	22.7	1.27
6	27.3	1.17
7	31.8	1.08
8	36.4	1.00
9	40.9	0.92
10	45.5	0.84
11	50.0	0.77

APPENDIX B: Formulae for estimation of genetic and phenotypic parameters and standard errors.

Term

s = number of sites
r = number of replications within sites
m = number of male pollen trees
f = number of female seed trees
t = number of trees within plots

Variance components

σ^2_w = variance among trees within plots
σ^2_{rmf} = variance among full-sib family plots within sites
σ^2_{smf} = variance among site-male-female combinations
σ^2_{mf} = variance among male-female combinations
σ^2_{rf} = variance among rep-female combinations within sites
σ^2_{rm} = variance among rep-male combinations within sites
σ^2_{sf} = variance among site-female combinations
σ^2_{sm} = variance among site-male combinations
σ^2_f = variance among female half-sib families
σ^2_m = variance among male half-sib families
σ^2_r = variance among replications within sites
σ^2_s = variance among sites

k_i = coefficient of the "i"th variance component

I. VARIANCE COMPONENTS (based on Table 3)

$$\sigma^2_{m} = (MS_3 - k_{16}\sigma^2_{sm} - k_{25}\sigma^2_{rm} - k_{23}\sigma^2_{mf} - k_{29}\sigma^2_{smf} - k_{30}\sigma^2_{rmf} - \sigma^2_{w})/k_6$$

$$\sigma^2_{f} = (MS_4 - k_{20}\sigma^2_{sf} - k_{27}\sigma^2_{rf} - k_{23}\sigma^2_{mf} - k_{29}\sigma^2_{smf} - k_{30}\sigma^2_{rmf} - \sigma^2_{w})/k_{12}$$

$$\sigma^2_{sm} = (MS_5 - k_{25}\sigma^2_{rm} - k_{29}\sigma^2_{smf} - k_{30}\sigma^2_{rmf} - \sigma^2_{w})/k_{16}$$

$$\sigma^2_{sf} = (MS_6 - k_{27}\sigma^2_{rf} - k_{29}\sigma^2_{smf} - k_{30}\sigma^2_{rmf} - \sigma^2_{w})/k_{20}$$

$$\sigma^2_{mf} = (MS_7 - k_{29}\sigma^2_{smf} - k_{30}\sigma^2_{rmf} - \sigma^2_{w})/k_{23}$$

$$\sigma^2_{rm} = (MS_8 - k_{30}\sigma^2_{rmf} - \sigma^2_{w})/k_{25}$$

$$\sigma^2_{rf} = (MS_9 - k_{30}\sigma^2_{rmf} - \sigma^2_{w})/k_{27}$$

$$\sigma^2_{smf} = (MS_{10} - k_{30}\sigma^2_{rmf} - \sigma^2_{w})/k_{29}$$

$$\sigma^2_{rmf} = (MS_{11} - \sigma^2_{w})/k_{30}$$

$$\sigma^2_{w} = MS_{12}$$

II. GENETIC / PHENOTYPIC PARAMETERS

σ_A^2 = additive genetic variance = $4\sigma_f^2$

σ_D^2 = dominance genetic variance = $4\sigma_{mf}^2$

σ_{Pi}^2 = phenotypic variance among individuals

$$= \sigma_m^2 + \sigma_f^2 + \sigma_{mf}^2 + \sigma_{sm}^2 + \sigma_{sf}^2 + \sigma_{rm}^2 + \sigma_{rf}^2 + \sigma_{smf}^2 + \sigma_{rmf}^2 + \sigma_w^2$$

σ_{PHS}^2 = phenotypic variance among half-sib means

$$= \sigma_f^2 + \frac{k_{23}}{k_{12}}\sigma_{mf}^2 + \frac{k_{20}}{k_{12}}\sigma_{sf}^2 + \frac{k_{27}}{k_{12}}\sigma_{rf}^2 + \frac{k_{29}}{k_{12}}\sigma_{smf}^2 + \frac{k_{30}}{k_{12}}\sigma_{rmf}^2 + \frac{1}{k_{12}}\sigma_w^2$$

h_i^2 = individual tree heritability = $\dfrac{\sigma_A^2}{\sigma_{Pi}^2}$

h_f^2 = half-sib family heritability = $\dfrac{\frac{1}{4}\sigma_A^2}{\sigma_{PHS}^2}$

II. GENETIC / PHENOTYPIC PARAMETERS (continued)

$COV_A(X,Y)$ = additive genetic covariance between X and Y

$=4\ COV_f$

$COV(f,PHS)$ = covariance of the breeding value of a seed parent and its half-sib family mean phenotypic value

$= \frac{1}{2}\sigma_A^2$

or for different characters (X,Y)

$= \frac{1}{2}COV_A$

$COV_P(X,Y)$ = phenotypic covariance between X and Y (calculated as per either σ^2_{Pi} or σ^2_{PHS})

r_A = additive genetic correlation of X and Y

$= COV_A(X,Y) \div [\sigma_A(X) \times \sigma_A(Y)]$

r_P = phenotypic correlation of X and Y (Pi or PHS)

$= COV_P(X,Y) \div [\sigma_P(X) \times \sigma_P(Y)]$

r_E = environmental correlation

$= [r_P - h_X h_Y r_A] \div [(1-h_X)(1-h_Y)]$

II. GENETIC / PHENOTYPIC PARAMETERS (continued)

CR_Y = correlated response of character Y is

= $ih_X h_Y r_A \sigma_P(Y)$

III. STANDARD ERRORS OF COMPONENTS/PARAMETERS

$S(\sigma_i^2)$ = the standard error of the i^{th} component

$$= \frac{2}{k_i^2} \sum_j \frac{MS_j^2}{f_j + 2}$$

where k_i is the coefficient of the variance component being estimated, MS_j is the j^{th} mean square used to estimate the variance component and f_j are the degrees of freedom of the j^{th} mean square.

$S(\sigma_A^2)$ = $4 * S(\sigma_f^2)$

III. STANDARD ERRORS OF COMPONENTS/PARAMETERS (continued)

$$S(h_i^2) = \frac{S(\sigma_A^2)}{\sigma_{Pi}^2}$$

$$S(h_f^2) = \frac{S(\sigma_f^2)}{\sigma_{PHS}^2}$$

$$S(r_A) = \frac{1 - r_A^2}{\sqrt{2}} \sqrt{\left[\frac{S(h_X^2)\ S(h_Y^2)}{h_X^2\ h_Y^2}\right]}$$

The formulae for standard errors of variance components and approximations of standard errors of heritabilities and genetic correlations are from Becker (1975).

IV. FORM OF MATRIX FOR MULTIPLE TRAIT PROGENY TEST SELECTION

i. variance/covariance matrix of phenotypic values **P**

$$\begin{matrix} \sigma^2_{PHS}X & COV_{PHS}(X,Y) \\ COV_{PHS}(X,Y) & \sigma^2_{PHS}Y \end{matrix}$$

ii. additive genetic variance/covariance matrix **G**

$$\begin{matrix} \tfrac{1}{2}\sigma^2_A\ X & \tfrac{1}{2}COV_A(X,Y) \\ \tfrac{1}{2}COV_A(X,Y) & \tfrac{1}{2}\sigma^2_A\ Y \end{matrix}$$

iii. b values are:

$$\mathbf{P}^{-1}\mathbf{G}\mathbf{a},$$

where a is a vector of economic weights

APPENDIX C: Tables of means and analyses of variance and covariance for growth and yield traits.

TABLE C1. Means and coefficients of variation for height at 6 years (HT06) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

	CLES			GVWS			COMBINED		
GROUP	N	MEAN cm	CV %	N	MEAN cm	CV %	N	MEAN cm	CV %
SEED PARENTS									
415	104	98.55	24.36	92	85.79	28.28	196	92.56	26.90
300	104	109.67	25.71	91	80.89	34.66	195	96.24	32.76
49	106	106.10	31.57	92	87.41	30.17	198	97.41	32.57
72	106	107.21	24.57	91	93.08	27.81	197	100.68	26.82
60	105	111.34	25.72	101	96.74	31.00	206	104.18	28.93
422	106	112.64	25.44	102	95.76	32.93	208	104.37	29.90
110	104	110.36	23.27	97	98.66	27.15	201	104.72	25.59
323	106	112.16	25.32	93	98.17	30.52	199	105.62	28.30
305	100	108.70	27.77	90	103.84	30.15	190	106.40	28.89
73	106	113.10	26.55	90	98.67	31.75	196	106.48	29.48
315	107	118.18	22.72	92	95.14	30.27	199	107.53	27.90
57	106	117.03	24.43	95	97.97	35.13	201	108.02	30.38
310	107	114.07	26.52	90	101.25	30.21	197	108.22	28.65
193	105	116.19	25.16	100	103.50	26.79	205	110.00	26.49
303	103	111.38	24.46	99	109.42	33.13	202	110.42	28.90
418	103	120.93	24.18	96	102.08	32.14	199	111.84	28.92
549	106	118.59	25.81	92	105.43	30.02	198	112.48	28.19
408	107	118.51	24.20	94	106.66	33.41	201	112.97	28.84
314	105	116.54	21.44	100	109.81	26.03	205	113.26	23.79
499	103	112.60	23.18	103	116.21	29.03	206	114.40	26.35
439	104	120.12	23.11	100	110.93	29.71	204	115.61	26.55
623	107	123.65	25.17	96	111.69	27.73	203	118.00	26.74
POLLEN PARENTS									
24	574	111.23	26.57	516	95.70	32.56	1090	103.88	30.12
62	579	111.15	24.05	534	98.10	31.80	11[illegible]	104.89	28.29
33	582	113.62	26.43	525	103.27	30.43	1107	108.71	28.62
448	575	118.24	24.18	521	105.36	30.47	1096	112.11	27.63
TOTAL	2310	113.56	25.43	2096	100.61	31.49	4406	107.40	28.80

TABLE C2. Combined sites analysis of variance for height at 6 years (HT06).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	184185.88	72.491	68.755		7.18%		
REP/SITE	4	25485.47	32.197	20.069		3.19%		
MALE	4	15543.07	13.287	8.983		1.32%		
FEMALE	3	8416.44	31.202	13.225	5.201	3.09%	3.873	0.012
S * F	21	2343.44	1.997	1.000		0.20%	1.085	0.405
R * F	84	1900.72	0.0	10.075		0.0 %	1.000	0.488
M * F	63	1988.33	0.0	10.831		0.0 %	0.921	0.627
S*M*F	63	2158.89	9.662	16.680		0.96%	1.136	0.246
R/S*M*F	252	1900.47	144.956	20.517	11.211	14.36%	2.701	0.0
WITHIN	3878	703.65	703.656	15.976	24.699	69.71%		
ADDITIVE GENETIC VARIANCE			124.809	52.901	10.402			
DOMINANCE GENETIC VARIANCE			0.0	43.324	0.0			
TOTAL PHENOTYPIC VARIANCE			904.760		28.007			
PHENOTYPIC VARIANCE HALF-SIB			42.887		6.098			
PHENOTYPIC VARIANCE FULL-SIB			87.271					
HERITABILITY (INDIVIDUAL)			0.138	0.058		%RESPONSE/i =	3.864	
HERITABILITY (HALF-SIB)			0.728	0.308		%RESPONSE/i =	8.873	
HERITABILITY (FULL-SIB)			0.715	0.303				

TABLE C2 (Continued). Analysis of variance for trait HT06 on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	18712.00	22.279	17.255		2.58%		
MALE	3	6474.73	7.041	7.379		0.82%		
FEMALE	21	3418.01	19.628	10.647	3.901	2.27%	2.510	0.036
R * M	6	2202.48	2.114	5.840		0.25%	1.232	0.294
R * F	42	1151.33	0.0	9.512		0.0 %	0.644	0.949
M * F	63	1998.23	7.832	15.876		0.91%	1.118	0.296
R*M*F	126	1787.98	127.360	25.726	9.938	14.76%	2.643	0.0
WITHIN	2046	676.58	676.584	21.143	22.906	78.41%		
ADDITIVE GENETIC VARIANCE			78.512	42.590	7.803			
DOMINANCE GENETIC VARIANCE			31.327	63.505	4.929			
TOTAL PHENOTYPIC VARIANCE			840.558		25.531			
PHENOTYPIC VARIANCE HALF-SIB			38.616		5.472			
PHENOTYPIC VARIANCE FULL-SIB			102.698					
HERITABILITY (INDIVIDUAL)			0.093	0.051		%RESPONSE/i =	2.385	
HERITABILITY (HALF-SIB)			0.508	0.276		%RESPONSE/i =	5.563	
HERITABILITY (FULL-SIB)			0.336	0.207				

TABLE C2 (Continued). Analysis of variance for trait HT06 on site GVWS

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	32891.90	43.992	33.320		4.28%		
MALE	3	10442.10	16.810	12.723		1.63%		
FEMALE	21	7246.48	46.997	23.713	6.814	4.57%	2.599	0.010
R * M	6	1538.18	0.0	4.639		0.0 %	0.764	0.599
R * F	42	2663.59	19.401	19.637		1.89%	1.323	0.120
M * F	63	2137.94	4.151	19.116		0.40%	1.062	0.382
R*M*F	126	2012.97	163.323	32.278	12.702	15.88%	2.743	0.0
WITHIN	1832	733.89	733.890	24.235	26.926	71.35%		
ADDITIVE GENETIC VARIANCE			187.987	84.850	13.628			
DOMINANCE GENETIC VARIANCE			16.605	76.465	4.050			
TOTAL PHENOTYPIC VARIANCE			984.572		31.188			
PHENOTYPIC VARIANCE HALF-SIB			75.632		8.644			
PHENOTYPIC VARIANCE FULL-SIB			153.042					
HERITABILITY (INDIVIDUAL)			0.191	0.096		%RESPONSE/I =	5.955	
HERITABILITY (HALF-SIB)			0.621	0.314		%RESPONSE/I =	10.742	
HERITABILITY (FULL-SIB)			0.444	0.310				

TABLE C3. Means and coefficients of variation for height at 10 years (HT10) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

GROUP	CLES N	CLES MEAN cm	CLES CV %	GVWS N	GVWS MEAN cm	GVWS CV %	COMBINED N	COMBINED MEAN cm	COMBINED CV %
SEED PARENTS									
415	103	393.11	15.49	90	285.03	27.84	193	342.71	25.79
72	105	388.30	19.97	84	292.41	25.10	189	345.68	25.85
300	106	410.35	18.71	89	290.00	31.25	195	355.42	28.87
305	103	400.52	21.44	95	318.05	29.02	198	360.95	27.13
422	105	415.96	17.58	101	306.30	26.94	206	362.19	26.27
310	107	398.25	17.76	88	324.95	24.38	195	365.17	22.72
49	102	417.53	19.62	90	308.02	26.12	192	366.20	26.71
323	106	413.00	17.48	93	315.52	28.52	199	367.45	25.68
303	105	396.46	19.33	87	341.88	28.09	192	371.73	24.20
60	106	415.57	15.16	96	325.17	25.85	202	372.61	23.18
73	106	423.66	19.02	94	317.91	34.02	200	373.96	28.91
193	108	416.22	18.60	95	326.21	27.50	203	374.10	25.29
57	107	423.64	15.96	95	327.16	26.05	202	378.26	23.85
315	107	429.17	14.50	89	320.63	23.85	196	379.89	23.07
110	104	423.77	15.29	89	332.33	26.78	193	381.60	23.39
418	104	431.00	16.40	91	328.76	27.48	195	383.29	24.83
549	107	426.42	17.63	94	338.33	28.10	201	385.22	24.81
439	107	423.08	19.45	90	340.61	22.24	197	385.41	23.16
499	108	409.57	19.78	98	363.00	25.68	206	387.42	23.20
408	106	440.26	15.06	94	338.44	29.72	200	392.40	25.03
623	106	439.44	18.41	98	347.77	27.10	204	395.40	24.96
314	106	430.07	15.99	94	358.98	22.68	200	396.66	20.88
POLLEN PARENTS									
62	586	411.09	16.85	511	308.86	27.69	1097	363.47	25.47
33	580	409.81	18.97	507	328.73	26.75	1087	371.99	24.73
28	582	417.57	19.08	494	318.90	28.28	1076	372.27	26.30
448	576	428.32	16.54	522	343.72	26.87	1098	388.10	23.71
TOTAL	2324	416.66	17.96	2034	325.20	27.65	4358	373.97	25.14

TABLE C4. Combined sites analysis of variance for height at 10 years (HT10).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	9073866.00	4095.354	3415.600		36.17%		
REP/SITE	4	192391.88	232.665	153.433		2.05%		
MALE	4	125997.56	102.458	75.337		0.90%		
FEMALE	3	44047.42	209.854	74.268	3.874	1.85%	2.815	0.011 **
S * F	21	15666.64	0.0	1.000		0.0 %	0.655	0.853
R * F	84	17965.60	60.213	93.420		0.53%	1.138	0.223
M * F	63	8738.00	0.0	87.760		0.0 %	0.402	1.000
S*M*F	63	21738.80	238.032	165.679		2.10%	1.377	0.045
R/S*M*F	252	15788.31	1315.176	171.973	9.697	11.62%	3.134	0.0
WITHIN	3830	5038.02	5038.023	115.096	18.980	44.50%		
ADDITIVE GENETIC VARIANCE			839.416	297.072	7.747			
DOMINANCE GENETIC VARIANCE			0.0	351.041	0.0			
TOTAL PHENOTYPIC VARIANCE			6993.934		22.363			
PHENOTYPIC VARIANCE HALF-SIB			329.054		4.851			
PHENOTYPIC VARIANCE FULL-SIB			749.286					
HERITABILITY (INDIVIDUAL)			0.120	0.042		%RESPONSE/i =	2.684	
HERITABILITY (HALF-SIB)			0.638	0.226		%RESPONSE/i =	6.187	
HERITABILITY (FULL-SIB)			0.560	0.198				

** MS S*F USED AS ERROR MS

TABLE C4 (Continued). Analysis of variance for trait HT10 on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	271974.00	330.285	248.523		5.76%		
MALE	3	40742.10	39.415	46.790		0.69%		
FEMALE	21	21968.30	74.318	72.034	2.069	1.30%	1.554	0.149
R * M	6	16274.10	18.432	42.814		0.32%	1.286	0.268
R * F	42	12545.30	0.0	88.379		0.0 %	0.991	0.497
M * F	63	14245.80	59.264	112.219		1.03%	1.126	0.285
R*M*F	126	12654.50	956.513	180.709	7.423	16.69%	2.976	0.0
WITHIN	2060	4252.65	4252.648	132.443	15.651	74.21%		
ADDITIVE GENETIC VARIANCE			297.271	288.135	4.138			
DOMINANCE GENETIC VARIANCE			237.055	448.876	3.695			
TOTAL PHENOTYPIC VARIANCE			5400.582		17.637			
PHENOTYPIC VARIANCE HALF-SIB			208.935		3.469			
PHENOTYPIC VARIANCE FULL-SIB			652.690					
HERITABILITY (INDIVIDUAL)			0.055	0.053		%RESPONSE/i =	0.971	
HERITABILITY (HALF-SIB)			0.356	0.345		%RESPONSE/i =	2.468	
HERITABILITY (FULL-SIB)			0.265	0.221				

TABLE C4 (Continued). Analysis of variance for trait HT10 on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	111292.69	121.775	117.682		1.46%		
MALE	3	112054.19	177.298	141.687		2.13%		
FEMALE	21	37990.39	188.939	138.584	4.227	2.27%	1.823	0.088 **
R * M	6	24749.39	31.509	74.455		0.38%	1.308	0.258
R * F	42	23289.47	128.389	179.099		1.54%	1.231	0.190
M * F	63	16468.54	0.0	162.188		0.0 %	0.870	0.728
R*M*F	126	18922.09	1713.247	313.567	12.728	20.61%	3.179	0.0
WITHIN	1770	5952.07	5952.074	199.964	23.724	71.60%		
ADDITIVE GENETIC VARIANCE			755.756	554.336	8.454			
DOMINANCE GENETIC VARIANCE			0.0	648.750	0.0			
TOTAL PHENOTYPIC VARIANCE			8191.449		27.831			
PHENOTYPIC VARIANCE HALF-SIB			436.290		6.423			
PHENOTYPIC VARIANCE FULL-SIB			1187.013					
HERITABILITY (INDIVIDUAL)			0.092	0.068		%RESPONSE/i =	2.568	
HERITABILITY (HALF-SIB)			0.433	0.318		%RESPONSE/i =	5.563	
HERITABILITY (FULL-SIB)			0.309	0.234				

** significant (P<.05) using M*F as error mean square

TABLE C5. Means and coefficients of variation for height at 12 years (HT12) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

	CLES			GVWS			COMBINED		
GROUP	N	MEAN cm	CV %	N	MEAN cm	CV %	N	MEAN cm	CV %
SEED PARENTS									
72	102	612.11	14.39	77	457.27	20.13	179	545.50	21.64
415	101	618.76	12.57	87	469.23	21.13	188	549.56	21.02
422	104	641.39	13.04	94	485.00	19.66	198	567.15	20.92
300	106	645.33	14.75	83	481.45	21.66	189	573.36	22.37
305	100	632.25	15.54	89	514.21	21.08	189	576.67	20.57
49	101	653.42	14.26	84	487.98	18.54	185	578.30	21.34
303	105	616.30	15.03	85	531.65	21.96	190	578.43	19.38
323	106	639.44	15.24	88	505.97	22.72	194	578.90	21.55
310	106	629.58	13.06	78	510.59	19.27	184	579.14	18.46
418	104	646.25	12.63	87	502.47	21.36	191	580.76	20.36
193	106	647.31	14.16	87	502.89	21.92	193	582.21	21.20
60	105	654.67	11.74	93	507.67	20.34	198	585.62	19.85
57	107	646.22	12.26	91	518.13	20.19	198	587.35	19.01
73	105	653.90	14.44	89	510.06	23.18	194	587.91	21.74
439	102	653.97	13.28	90	523.17	19.93	192	592.66	19.48
110	103	659.61	13.11	83	523.07	22.03	186	598.68	20.21
315	104	665.05	10.45	83	519.10	16.27	187	600.27	17.56
499	105	641.46	14.25	90	568.00	18.07	195	607.55	17.00
549	107	665.37	14.36	88	541.76	21.13	195	609.59	19.87
408	107	671.78	12.03	90	538.11	21.47	197	610.71	19.41
623	105	674.67	13.07	91	540.05	21.61	196	612.17	19.98
314	105	676.62	12.49	89	553.93	18.94	194	620.34	18.11
POLLEN PARENTS									
62	581	644.99	12.74	487	492.67	20.94	1068	575.53	20.76
33	572	634.08	14.31	485	514.22	19.99	1057	579.09	19.59
28	573	647.73	14.37	460	507.19	21.73	1033	585.15	20.99
448	570	663.86	13.01	484	540.75	20.91	1054	607.32	19.25
TOTAL	2296	647.64	13.70	1916	513.76	21.16	4212	586.74	20.25

TABLE C6. Combined sites analysis of variance for height at 12 years (HT12).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	18720896.00	8854.547	7317.902		46.12%		
REP/SITE	4	210609.19	254.449	174.152		1.33%		
MALE	4	221620.75	170.230	138.439		0.89%		
FEMALE	3	72244.75	352.992	123.748	3.202	1.84%	3.215	0.005 **
S * F	21	22511.28	0.0	1.000		0.0 %	0.619	0.883
R * F	84	24964.95	52.919	135.578		0.28%	1.094	0.295
M * F	63	16870.17	0.0	146.173		0.0 %	0.493	0.997
S*M*F	63	34200.03	471.478	268.835		2.46%	1.499	0.016
R/S*M*F	252	22813.15	2021.027	258.700	7.662	10.53%	3.284	0.0
WITHIN	3684	6947.80	6947.801	161.839	14.206	36.19%		
ADDITIVE GENETIC VARIANCE			1411.969	494.994	6.404			
DOMINANCE GENETIC VARIANCE			0.0	584.691	0.0			
TOTAL PHENOTYPIC VARIANCE			10090.922		17.121			
PHENOTYPIC VARIANCE HALF-SIB			538.967		3.957			
PHENOTYPIC VARIANCE FULL-SIB			1232.482					
HERITABILITY (INDIVIDUAL)			0.140	0.049		%RESPONSE/i =	2.396	
HERITABILITY (HALF-SIB)			0.655	0.230		%RESPONSE/i =	5.183	
HERITABILITY (FULL-SIB)			0.573	0.201				

**: MS S*F USED AS ERROR MS

TABLE C6 (Continued). Analysis of variance for trait HT12 on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	366609.38	441.977	339.464		5.42%		
MALE	3	85079.19	83.730	98.126		1.03%		
FEMALE	21	33931.42	120.651	111.963	1.696	1.48%	1.583	0.139
R * M	6	31765.90	64.217	84.009		0.79%	1.641	0.141
R * F	42	16094.37	0.0	120.880		0.0 %	0.832	0.750
M * F	63	24689.40	200.173	190.360		2.45%	1.276	0.125
R*M*F	126	19354.04	1581.060	280.203	6.140	19.38%	3.416	0.0
WITHIN	2032	5666.47	5666.477	177.685	11.623	69.46%		
ADDITIVE GENETIC VARIANCE			482.604	447.851	3.392			
DOMINANCE GENETIC VARIANCE			800.692	761.442	4.369			
TOTAL PHENOTYPIC VARIANCE			7716.297		13.563			
PHENOTYPIC VARIANCE HALF-SIB			356.117		2.914			
PHENOTYPIC VARIANCE FULL-SIB			1146.761					
HERITABILITY (INDIVIDUAL)			0.063	0.058		%RESPONSE/i =	0.848	
HERITABILITY (HALF-SIB)			0.339	0.314		%RESPONSE/i =	1.974	
HERITABILITY (FULL-SIB)			0.353	0.195				

TABLE C6 (Continued). Analysis of variance for trait HT12 on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	60883.24	42.349	71.436		0.35%		
MALE	3	195062.56	350.016	259.501		2.93%		
FEMALE	21	60384.63	312.668	229.786	3.442	2.61%	1.784	0.081 **
R * M	6	27745.58	1.964	89.480		0.02%	1.056	0.393
R * F	42	33236.13	207.013	270.539		1.73%	1.265	0.161
M * F	63	26888.16	0.0	265.370		0.0 %	1.023	0.448
R*M*F	126	26272.25	2519.994	468.178	9.771	21.07%	3.082	0.0
WITHIN	1652	8523.86	8523.859	296.404	17.970	71.28%		
ADDITIVE GENETIC VARIANCE			1250.674	919.143	6.884			
DOMINANCE GENETIC VARIANCE			0.0	1061.481	0.0			
TOTAL PHENOTYPIC VARIANCE			11915.508		21.247			
PHENOTYPIC VARIANCE HALF-SIB			683.042		5.087			
PHENOTYPIC VARIANCE FULL-SIB			1874.165					
HERITABILITY (INDIVIDUAL)			0.105	0.077		%RESPONSE/i =	2.230	
HERITABILITY (HALF-SIB)			0.458	0.336		%RESPONSE/i =	4.657	
HERITABILITY (FULL-SIB)			0.354	0.245				

** significant (P<.05) using M*F as error mean square

TABLE C7. Means and coefficients of variation for height difference (HTD) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

GROUP	CLES N	CLES MEAN cm	CLES CV %	GVWS N	GVWS MEAN cm	GVWS CV %	COMBINED N	COMBINED MEAN cm	COMBINED CV %
SEED PARENTS									
72	102	216.70	16.13	77	166.78	19.49	179	195.23	21.48
418	104	215.25	17.55	87	178.68	21.22	191	198.59	21.11
422	104	222.75	14.11	94	175.25	19.20	198	200.20	20.08
193	106	228.34	15.05	87	176.72	22.74	193	205.07	21.98
439	102	222.14	17.53	90	185.99	30.28	192	205.20	24.88
415	101	222.65	15.11	87	185.03	20.74	188	205.24	19.71
57	107	222.58	12.40	91	187.26	17.96	198	206.35	17.05
303	105	219.39	16.20	85	190.75	23.24	190	206.57	20.38
73	105	227.49	13.67	89	182.80	20.53	194	206.99	19.69
49	101	233.49	12.27	84	177.26	21.48	185	207.96	20.90
305	100	225.03	16.27	89	189.78	21.60	189	208.43	20.38
323	106	226.44	17.40	88	188.90	21.48	194	209.41	21.02
310	106	230.31	18.82	78	182.14	24.94	184	209.89	23.90
300	106	234.58	18.20	83	187.27	23.25	189	213.80	22.91
60	105	240.02	10.90	93	184.79	22.12	198	214.08	20.39
110	103	234.88	16.74	83	189.47	21.82	186	214.62	21.47
623	105	232.21	14.08	91	194.75	20.71	196	214.82	19.04
315	104	233.68	19.34	83	194.23	14.32	187	216.17	19.94
499	105	227.34	12.61	90	203.55	19.07	195	216.36	16.49
408	107	232.34	13.96	90	201.44	16.31	197	218.23	16.50
549	107	238.95	14.84	88	199.99	19.31	195	221.37	18.81
314	105	243.94	16.95	89	195.05	22.65	194	221.51	22.15
POLLEN PARENTS									
33	572	221.59	16.65	485	183.41	20.87	1057	204.07	20.62
28	573	227.60	15.83	460	187.76	24.20	1033	209.86	21.47
62	581	232.28	14.99	487	183.54	20.07	1068	210.05	20.57
448	570	233.31	15.59	484	194.64	20.91	1054	215.56	19.93
TOTAL	2296	228.70	15.88	1916	187.32	21.68	4212	209.88	20.73

TABLE C8. Combined sites analysis of variance for height increment from years 10 to 12 (HTD).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	1788452.00	837.098	699.147		35.92%		
REP/SITE	4	35271.79	46.754	29.054		2.01%		
MALE	4	23355.61	15.529	14.597		0.67%		
FEMALE	3	9499.05	28.929	16.199	2.563	1.24%	2.401	0.033
S * F	21	3464.52	7.301	1.000		0.31%	1.239	0.280
R * F	84	2682.49	4.250	14.663		0.18%	1.069	0.342
M * F	63	3114.29	9.598	15.652		0.41%	1.188	0.248
S*M*F	63	2621.70	3.818	21.728		0.16%	1.045	0.397
R/S*M*F	252	2508.77	166.282	28.583	6.144	7.13%	2.085	0.0
WITHIN	3684	1203.43	1203.433	28.032	16.529	51.63%		
ADDITIVE GENETIC VARIANCE			115.717	64.798	5.125			
DOMINANCE GENETIC VARIANCE			38.391	62.610	2.952			
TOTAL PHENOTYPIC VARIANCE			1446.896		18.124			
PHENOTYPIC VARIANCE HALF-SIB			49.226		3.343			
PHENOTYPIC VARIANCE FULL-SIB			108.398					
HERITABILITY (INDIVIDUAL)			0.080	0.045		%RESPONSE/1 =	1.449	
HERITABILITY (HALF-SIB)			0.588	0.329		%RESPONSE/1 =	3.929	
HERITABILITY (FULL-SIB)			0.622	0.299				

TABLE C8 (Continued). Analysis of variance for trait HTD on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	36912.19	45.550	34.151		3.38%		
MALE	3	16468.13	23.360	18.287		1.73%		
FEMALE	21	5940.68	30.200	18.246	2.403	2.24%	2.125	0.033
R * M	6	2309.64	0.050	6.223		0.00%	1.010	0.422
R * F	42	2038.71	0.0	14.998		0.0 %	0.891	0.659
M * F	63	3044.57	28.640	23.267		2.12%	1.331	0.089
R*M*F	126	2287.45	139.250	33.260	5.160	10.32%	2.114	0.0[illegible]
WITHIN	2032	1081.86	1081.860	33.924	14.382	80.20%		
ADDITIVE GENETIC VARIANCE			120.800	72.984	4.806			
DOMINANCE GENETIC VARIANCE			114.560	93.070	4.680			
TOTAL PHE[illegible]PIC VARIANCE			1303.360		15.786			
PHENOTYPIC VARIANCE HALF-SIB			59.274		3.366			
PHENOTYPIC VARIANCE FULL-SIB			169.919					
HERITABILITY (INDIVIDUAL)			0.093	0.056		%RESPONSE/I =	1.463	
HERITABILITY (HALF-SIB)			0.509	0.308		%RESPONSE/I =	3.430	
HERITABILITY (FULL-SIB)			0.484	0.215				

TABLE C8 (Continued). Analysis of variance for trait HTD on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	33952.14	48.550	37.674		2.89%		
MALE	3	13760.54	23.920	18.389		1.42%		
FEMALE	21	6933.30	42.560	25.741	3.483	2.53%	2.113	0.040
R * M	6	2428.28	0.0	7.920		0.0 %	0.889	0.505
R * F	42	3332.56	18.210	27.341		1.08%	1.221	0.199
M * F	63	2678.76	0.0	26.874		0.0 %	0.981	0.525
R*M*F	126	2730.09	195.530	48.933	7.465	11.63%	2.018	0.0
WITHIN	1652	1352.96	1352.960	47.047	19.636	80.45%		
ADDITIVE GENETIC VARIANCE			170.240	102.963	6.965			
DOMINANCE GENETIC VARIANCE			0.0	107.497	0.0			
TOTAL PHENOTYPIC VARIANCE			1633.179		21.574			
PHENOTYPIC VARIANCE HALF-SIB			79.944		4.773			
PHENOTYPIC VARIANCE FULL-SIB			192.379					
HERITABILITY (INDIVIDUAL)			0.104	0.063		%RESPONSE/I =	2.249	
HERITABILITY (HALF-SIB)			0.532	0.322		%RESPONSE/I =	5.082	
HERITABILITY (FULL-SIB)			0.346	0.268				

TABLE C9. Analysis of variance for trait HT12 on site CLES after reblocking.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	1374082.00	1792.620	1275.755		21.34%		
MALE	3	80120.44	93.810	89.313		1.12%		
FEMALE	21	34025.28	79.370	107.617	1.375	0.94%	1.318	0.202
R * M	6	7805.74	7.410	20.945		0.09%	1.222	0.299
R * F	42	7360.57	27.960	51.153		0.33%	1.153	0.271
M * F	63	25072.13	719.800	172.379		8.57%	3.926	0.000
R*M*F	126	6385.69	92.520	94.927	1.485	1.10%	1.143	0.139
WITHIN	2021	5588.74	5588.738	175.724	11.541	66.52%		
ADDITIVE GENETIC VARIANCE			317.480	430.467	2.751			
DOMINANCE GENETIC VARIANCE			2879.200	689.518	8.284			
TOTAL PHENOTYPIC VARIANCE			6609.594		12.551			
PHENOTYPIC VARIANCE HALF-SIB			330.008		2.804			
PHENOTYPIC VARIANCE FULL-SIB			1139.043					
HERITABILITY (INDIVIDUAL)			0.048	0.065		%RESPONSE/I =	0.603	
HERITABILITY (HALF-SIB)			0.241	0.326		%RESPONSE/I =	1.349	
HERITABILITY (FULL-SIB)			0.784	0.189				

TABLE C9 (Continued). Analysis of variance for trait HT12 of top 5 trees per full-sib family plot on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	224594.31	476.710	361.565		10.48%		
MALE	3	43433.06	71.930	87.956		1.58%		
FEMALE	21	21294.94	179.790	118.504	1.936	3.95%	2.025	0.064
R * M	6	17915.25	57.140	82.501		1.26%	1.540	0.170
R * F	42	8718.21	0.0	118.044		0.0 %	0.750	0.858
M * F	63	13429.79	119.860	184.612		2.63%	1.155	0.246
R*M*F	126	11630.99	1998.680	291.127	6.455	43.92%	7.065	0.0
WITHIN	1055	1646.32	1646.320	71.613	5.858	36.18%		
ADDITIVE GENETIC VARIANCE			719.160	474.017	3.872			
DOMINANCE GENETIC VARIANCE			479.440	738.449	3.161			
TOTAL PHENOTYPIC VARIANCE			4073.719		9.215			
PHENOTYPIC VARIANCE HALF-SIB			403.750		2.901			
PHENOTYPIC VARIANCE FULL-SIB			1147.561					
HERITABILITY (INDIVIDUAL)			0.177	0.116		%RESPONSE/i =	1.627	
HERITABILITY (HALF-SIB)			0.445	0.294		%RESPONSE/i =	2.584	
HERITABILITY (FULL-SIB)			0.324	0.207				

TABLE C9 (Continued). Analysis of variance for trait HT12 of top 4 trees per full-sib family plot on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	181902.31	484.615	365.990		11.41%		
MALE	3	33652.97	72.894	85.168		1.72%		
FEMALE	21	17813.21	209.987	122.581	2.061	4.94%	2.303	0.047
R * M	6	13833.33	47.265	79.794		1.11%	1.430	0.208
R * F	42	7158.28	0.0	121.764		0.0 %	0.740	0.868
M * F	63	10249.52	47.961	180.640		1.13%	1.059	0.386
R*M*F	126	9674.00	2096.177	302.745	6.513	49.34%	7.503	0.0
WITHIN	792	1289.29	1289.291	64.708	5.108	30.35%		
ADDITIVE GENETIC VARIANCE			839.949	490.324	4.123			
DOMINANCE GENETIC VARIANCE			191.842	722.562	1.970			
TOTAL PHENOTYPIC VARIANCE			3763.575		8.727			
PHENOTYPIC VARIANCE HALF-SIB			423.519		2.927			
PHENOTYPIC VARIANCE FULL-SIB			1137.008					
HERITABILITY (INDIVIDUAL)			0.223	0.130		%RESPONSE/i =	1.948	
HERITABILITY (HALF-SIB)			0.496	0.289		%RESPONSE/i =	2.903	
HERITABILITY (FULL-SIB)			0.291	0.216				

TABLE C10. Means and coefficients of variation for diameter at 6 years (DM06) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

GROUP	CLES N	 MEAN mm	 CV %	GVWS N	 MEAN mm	 CV %	COMBINED N	 MEAN mm	 CV %
SEED PARENTS									
300	104	19.12	25.29	91	13.30	34.29	195	16.40	33.69
60	105	19.61	24.11	101	14.60	36.32	206	17.16	32.64
415	104	19.18	25.72	91	15.35	31.49	195	17.39	30.11
49	106	20.08	31.08	92	14.84	33.92	198	17.64	35.54
73	106	20.32	26.47	90	15.99	36.80	196	18.33	32.76
305	100	19.28	27.43	90	17.83	33.42	190	18.59	30.37
422	106	20.86	26.05	102	16.81	38.49	208	18.88	33.31
408	107	20.64	24.76	94	17.10	37.87	201	18.98	31.81
57	106	21.58	23.06	95	16.16	33.53	201	19.02	30.74
315	107	21.58	22.82	92	16.04	32.54	199	19.02	30.28
110	104	20.64	23.60	97	17.58	35.35	201	19.16	30.03
72	106	21.23	25.06	91	16.86	29.23	197	19.21	29.02
323	106	20.82	23.59	93	17.55	31.51	199	19.29	28.24
310	107	21.09	25.61	90	17.51	33.01	197	19.46	30.04
623	107	21.00	23.91	96	17.98	29.52	203	19.57	27.40
499	103	20.84	18.84	103	18.36	31.14	206	19.60	25.76
303	103	21.05	25.04	99	18.71	35.73	202	19.90	30.67
193	105	21.60	23.81	100	18.13	29.42	205	19.91	27.66
314	105	21.96	20.76	100	19.10	29.28	205	20.57	25.65
418	103	22.79	22.20	96	18.41	34.40	199	20.67	29.51
549	106	22.97	23.32	92	19.46	30.99	198	21.34	27.80
439	104	23.67	23.26	100	19.91	32.73	204	21.83	28.85
POLLEN PARENTS									
28	574	20.55	25.00	516	16.48	34.89	1090	18.62	31.16
62	579	20.58	23.70	534	16.73	34.47	1113	18.73	30.20
448	575	21.39	24.67	520	17.51	33.49	1095	19.55	30.13
33	582	21.48	25.73	525	18.04	34.38	1107	19.85	30.74
TOTAL	2310	21.00	24.88	2095	17.19	34.48	4405	19.19	30.67

TABLE C11. Combined sites analysis of variance for diameter at 6 years (DM06).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	15952.34	6.725	5.937		17.27%		
REP/SITE	4	1260.08	1.608	0.992		4.13%		
MALE	4	396.86	0.351	0.230		0.90%		
FEMALE	3	347.42	1.455	0.533	6.287	3.74%	6.156	0.006
S * F	21	62.32	0.0	1.000		0.0 %	0.688	0.821
R * F	84	77.79	0.272	0.400		0.70%	1.146	0.211
M * F	63	74.83	0.0	0.404		0.0 %	0.927	0.618
S*M*F	63	80.71	0.489	0.619		1.26%	1.189	0.178
R/S*M*F	252	67.85	5.489	0.732	12.210	14.09%	3.009	0.0
WITHIN	3877	22.55	22.551	0.512	24.750	57.90%		
ADDITIVE GENETIC VARIANCE			5.820	2.132	12.574			
DOMINANCE GENETIC VARIANCE			0.0	1.618	0.0			
TOTAL PHENOTYPIC VARIANCE			30.616		28.838			
PHENOTYPIC VARIANCE HALF-SIB			1.900		7.184			
PHENOTYPIC VARIANCE FULL-SIB			3.406					
HERITABILITY (INDIVIDUAL)			0.190	0.070		%RESPONSE/i =	5.482	
HERITABILITY (HALF-SIB)			0.766	0.280		%RESPONSE/i =	11.004	
HERITABILITY (FULL-SIB)			0.855	0.313				

TABLE C11 (Continued). Analysis of variance for trait DMO6 on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	1207.05	1.537	1.109		5.38%		
MALE	3	150.67	0.162	0.171		0.57%		
FEMALE	21	148.31	0.946	0.444	4.633	3.31%	3.022	0.012
R * M	6	44.48	0.0	0.121		0.0 %	0.780	0.587
R * F	42	36.56	0.0	0.303		0.0 %	0.641	0.951
M * F	63	69.56	0.471	0.540		1.65%	1.219	0.174
R*M*F	126	57.05	4.091	0.821	9.632	14.33%	2.672	0.0
WITHIN	2046	21.35	21.350	0.667	22.003	74.76%		
ADDITIVE GENETIC VARIANCE			3.786	1.776	9.266			
DOMINANCE GENETIC VARIANCE			1.885	2.159	6.537			
TOTAL PHENOTYPIC VARIANCE			27.021		24.754			
PHENOTYPIC VARIANCE HALF-SIB			1.608		6.038			
PHENOTYPIC VARIANCE FULL-SIB			3.756					
HERITABILITY (INDIVIDUAL)			0.140	0.066		%RESPONSE/I =	3.468	
HERITABILITY (HALF-SIB)			0.589	0.276		%RESPONSE/I =	7.110	
HERITABILITY (FULL-SIB)			0.421	0.236				

TABLE C11 (Continued). Analysis of variance for trait DM06 on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	1358.39	1.752	1.378		4.88%		
MALE	3	272.40	0.328	0.343		0.91%		
FEMALE	21	255.97	1.371	0.858	6.813	3.82%	2.022	0.037
R * M	6	95.28	0.083	0.279		0.23%	1.211	0.305
R * F	42	119.71	1.237	0.865		3.45%	1.522	0.039
M * F	63	85.57	0.211	0.756		0.59%	1.088	0.341
R*M*F	126	78.66	7.031	1.268	15.426	19.58%	3.292	0.0
WITHIN	1831	23.89	23.894	0.789	28.438	66.54%		
ADDITIVE GENETIC VARIANCE			5.485	3.432	13.625			
DOMINANCE GENETIC VARIANCE			0.844	3.025	5.345			
TOTAL PHENOTYPIC VARIANCE			34.156		34.000			
PHENOTYPIC VARIANCE HALF-SIB			2.661		9.490			
PHENOTYPIC VARIANCE FULL-SIB			5.220					
HERITABILITY (INDIVIDUAL)			0.161	0.100		%RESPONSE/i =	5.460	
HERITABILITY (HALF-SIB)			0.515	0.322		%RESPONSE/i =	9.782	
HERITABILITY (FULL-SIB)			0.366	0.329				

TABLE C12. Means and coefficients of variation for diameter at 10 years (DM10) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

	CLES			GVWS			COMBINED		
GROUP	N	MEAN mm	CV %	N	MEAN mm	CV %	N	MEAN mm	CV %
SEED PARENTS									
415	103	62.96	18.41	90	45.84	28.06	193	54.98	27.06
300	106	67.85	20.76	89	42.91	31.86	195	56.47	33.00
60	106	68.33	18.16	96	48.14	31.35	202	58.73	29.01
422	105	70.56	21.29	101	49.08	30.01	206	60.03	30.55
49	102	71.53	23.67	90	47.76	30.39	192	60.39	32.76
305	103	67.46	24.33	95	53.17	30.19	198	60.60	29.22
73	106	70.49	22.62	94	49.60	34.26	200	60.67	32.06
323	106	69.58	19.87	93	52.10	30.07	199	61.41	27.82
315	107	71.39	18.37	89	49.58	23.64	196	61.49	26.92
303	105	67.90	21.86	87	54.34	30.86	192	61.76	27.69
72	105	70.23	21.58	84	51.58	30.51	189	61.94	29.00
57	107	71.73	18.37	95	52.36	27.01	202	62.62	26.68
110	104	71.68	21.22	89	53.57	29.48	193	63.33	28.26
499	108	67.94	22.34	98	58.68	26.46	206	63.53	25.17
408	106	71.54	19.12	94	54.88	31.89	200	63.71	27.69
623	106	72.98	21.67	98	55.14	29.05	204	64.41	28.28
310	107	71.43	21.57	88	55.97	28.46	195	64.45	27.00
418	104	72.44	16.93	91	55.84	29.38	195	64.69	25.57
193	108	73.40	20.45	95	55.23	29.15	203	64.90	27.67
549	107	73.13	20.32	94	55.94	30.22	201	65.09	27.65
314	106	75.35	17.23	94	59.89	24.22	200	68.09	23.09
439	107	77.15	20.64	90	59.28	27.58	197	68.98	26.66
POLLEN PARENTS									
28	582	70.16	21.16	494	50.40	31.84	1076	61.09	29.93
62	586	71.36	20.25	511	51.64	30.30	1097	62.17	28.87
33	580	70.63	22.46	507	54.14	29.28	1087	62.94	28.38
448	576	71.01	19.61	522	54.89	29.15	1098	63.35	26.80
TOTAL	2324	70.79	20.89	2034	52.79	30.26	4358	62.39	28.51

TABLE C13. Combined sites analysis of variance for diameter at 10 years (DM10).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	351291.00	157.765	132.239		38.78%		
REP/SITE	4	8698.29	11.239	6.924		2.76%		
MALE	4	1318.69	0.622	0.984		0.15%		
FEMALE	3	2122.32	9.521	3.371	4.946	2.34%	3.661	0.002 **
S * F	21	579.38	0.0	1.000		0.0 %	0.962	0.528
R * F	84	533.99	0.0	2.921		0.0 %	0.926	0.656
M * F	63	306.46	0.0	2.737		0.0 %	0.475	0.998
S*M*F	63	645.52	2.625	5.071		0.65%	1.119	0.271
R/S*M*F	252	576.96	49.142	6.286	11.236	12.08%	3.292	0.0
WITHIN	3830	175.27	175.271	4.004	21.219	43.09%		
ADDITIVE GENETIC VARIANCE			38.086	13.484	9.891			
DOMINANCE GENETIC VARIANCE			0.0	10.948	0.0			
TOTAL PHENOTYPIC VARIANCE			237.800		24.716			
PHENOTYPIC VARIANCE HALF-SIB			12.758		5.725			
PHENOTYPIC VARIANCE FULL-SIB			23.098					
HERITABILITY (INDIVIDUAL)			0.160	0.057		%RESPONSE/i =	3.958	
HERITABILITY (HALF-SIB)			0.746	0.264		%RESPONSE/i =	8.545	
HERITABILITY (FULL-SIB)			0.824	0.292				

** MS S*F USED AS ERROR MS

TABLE C13 (Continued). Analysis of variance for trait DM10 on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP.	2	14420.80	17.830	13.172		7.82%		
MALE	3	158.03	0.0	0.643		0.0 %		
FEMALE	21	959.85	4.894	3.018	3.125	2.15%	2.163	0.056
R * M	6	684.38	0.843	1.799		0.37%	1.318	0.254
R * F	42	445.57	0.0	3.272		0.0 %	0.858	0.710
M * F	63	517.38	0.0	4.234		0.0 %	0.997	0.496
R*M*F	126	519.13	40.441	7.410	8.983	17.74%	3.167	0.0
WITHIN	2060	163.91	163.906	5.105	18.085	71.92%		
ADDITIVE GENETIC VARIANCE			19.577	12.072	6.250			
DOMINANCE GENETIC VARIANCE			0.0	16.934	0.0			
TOTAL PHENOTYPIC VARIANCE			210.084		20.475			
PHENOTYPIC VARIANCE HALF-SIB			9.810		4.424			
PHENOTYPIC VARIANCE FULL-SIB			24.573					
HERITABILITY (INDIVIDUAL)			0.093	0.057		%RESPONSE/i =	1.908	
HERITABILITY (HALF-SIB)			0.499	0.308		%RESPONSE/i =	4.415	
HERITABILITY (FULL-SIB)			0.199	0.246				

TABLE C13 (Continued). Analysis of variance for trait DM10 on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	2769.17	3.431	2.915		1.27%		
MALE	3	2234.98	3.866	2.828		1.44%		
FEMALE	21	1743.10	14.423	5.863	7.193	5.36%	4.123	0.010
R * M	6	477.87	0.0	1.488		0.0 %	0.753	0.608
R * F	42	615.54	0.0	4.995		0.0 %	0.970	0.532
M * F	63	442.05	0.0	4.820		0.0 %	0.696	0.944
R*M*F	126	634.79	58.952	10.515	14.543	21.90%	3.368	0.0
WITHIN	1770	188.50	188.499	6.333	26.005	70.03%		
ADDITIVE GENETIC VARIANCE			57.692	23.452	14.387			
DOMINANCE GENETIC VARIANCE			0.0	19.282	0.0			
TOTAL PHENOTYPIC VARIANCE			265.739		30.877			
PHENOTYPIC VARIANCE HALF-SIB			21.289		8.740			
PHENOTYPIC VARIANCE FULL-SIB			45.824					
HERITABILITY (INDIVIDUAL)			0.217	0.088		%RESPONSE/i =	6.703	
HERITABILITY (HALF-SIB)			0.677	0.275		%RESPONSE/i =	11.842	
HERITABILITY (FULL-SIB)			0.399	0.256				

TABLE C14. Means and coefficients of variation for diameter at 12 years (DM12) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

	CLES			GVWS			COMBINED		
GROUP	N	MEAN mm	CV %	N	MEAN mm	CV %	N	MEAN mm	CV %
SEED PARENTS									
415	101	80.58	11.53	78	60.61	22.41	179	71.88	20.95
323	106	83.04	15.40	87	62.76	20.35	193	73.90	22.02
57	107	82.97	12.74	91	63.36	19.08	198	73.96	20.19
305	100	83.75	15.08	88	63.62	22.13	188	74.33	22.44
300	106	85.22	14.78	83	61.91	22.71	189	74.98	23.46
60	105	84.30	14.53	85	65.18	17.74	190	75.75	20.14
499	105	81.65	14.97	87	69.86	17.20	192	76.31	17.62
303	105	83.31	15.73	84	67.71	20.24	189	76.37	20.21
422	104	86.11	12.49	84	64.42	16.96	188	76.42	20.00
418	104	85.17	13.59	84	66.01	19.50	188	76.61	20.16
549	107	85.80	14.95	88	66.37	21.38	195	77.03	21.49
72	102	86.55	15.15	74	64.52	17.77	176	77.29	21.38
73	105	88.52	13.86	89	64.15	24.29	194	77.34	23.85
408	107	86.22	14.00	87	66.42	20.32	194	77.34	20.79
315	104	85.88	11.45	80	66.73	14.27	184	77.55	17.50
49	101	89.09	15.46	80	65.24	17.75	181	78.55	22.24
623	105	88.65	14.26	88	66.85	22.14	193	78.71	22.16
310	106	87.26	14.47	74	68.76	19.22	180	79.66	19.77
110	103	89.04	14.40	78	68.19	20.78	181	80.06	21.14
193	106	89.38	13.12	81	68.54	21.60	187	80.35	20.79
314	105	91.79	12.03	86	71.23	18.69	191	82.53	19.20
439	102	94.55	15.71	86	71.03	15.96	188	83.79	21.20
POLLEN PARENTS									
28	573	85.62	15.03	426	65.09	21.29	999	76.87	21.77
62	581	87.17	13.83	473	64.83	19.87	1054	77.14	21.61
33	572	86.50	15.35	473	66.71	19.57	1045	77.54	21.21
448	570	85.92	14.03	470	67.53	19.55	1040	77.61	20.05
TOTAL	2296	86.31	14.58	1842	66.06	20.10	4138	77.30	21.16

TABLE C15. Combined sites analysis of variance for diameter at 12 years (DM12).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	418722.00	202.338	167.262		53.18%		
REP/SITE	4	5093.36	6.675	4.279		1.75%		
MALE	4	343.52	0.0	0.554		0.0 %		
FEMALE	3	1458.35	7.047	2.441	3.434	1.85%	4.150	0.001 **
S * F	21	351.62	0.0	1.000		0.0 %	0.873	0.621
R * F	84	342.68	0.0	2.106		0.0 %	0.764	0.926
M * F	63	298.85	0.0	2.363		0.0 %	0.587	0.982
S*M*F	63	509.05	2.266	4.252		0.60%	1.134	0.249
R/S*M*F	251	148.82	43.023	5.209	8.486	11.31%	3.799	0.0
WITHIN	3611	118.13	118.127	2.779	14.061	31.05%		
ADDITIVE GENETIC VARIANCE			28.188	9.763	6.869			
DOMINANCE GENETIC VARIANCE			0.0	9.453	0.0			
TOTAL PHENOTYPIC VARIANCE			171.460		16.941			
PHENOTYPIC VARIANCE HALF-SIB			9.709		4.031			
PHENOTYPIC VARIANCE FULL-SIB			17.707					
HERITABILITY (INDIVIDUAL)			0.164	0.057		%RESPONSE/i =	2.785	
HERITABILITY (HALF-SIB)			0.726	0.251		%RESPONSE/i =	5.852	
HERITABILITY (FULL-SIB)			0.796	0.276				

** MS S*F USED AS ERROR MS

TABLE C15 (Continued). Analysis of variance for trait DM12 on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	5720.34	6.587	5.317		3.93%		
MALE	3	273.44	0.0	0.827		0.0 %		
FEMALE	21	1147.21	8.210	3.445	3.320	4.90%	3.912	0.012
R * M	6	860.60	1.948	2.272		1.16%	1.776	0.109
R * F	42	306.47	0.0	2.565		0.0 %	0.633	0.955
M * F	63	471.28	0.0	3.933		0.0 %	0.973	0.540
R*M*F	126	484.47	43.561	7.012	[illegible].647	25.98%	4.513	0.0
WITHIN	2032	107.35	107.350	3.366	12.005	64.03%		
ADDITIVE GENETIC VARIANCE			32.842	13.778	6.640			
DOMINANCE GENETIC VARIANCE			0.0	15.732	0.0			
TOTAL PHENOTYPIC VARIANCE			161.069		14.705			
PHENOTYPIC VARIANCE HALF-SIB			12.850		4.153			
PHENOTYPIC VARIANCE FULL-SIB			26.782					
HERITABILITY (INDIVIDUAL)			0.204	0.086		%RESPONSE/I =	2.998	
HERITABILITY (HALF-SIB)			0.639	0.268		%RESPONSE/I =	5.308	
HERITABILITY (FULL-SIB)			0.307	0.257				

TABLE C15 (Continued). Analysis of variance for trait DM12 on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	4603.30	7.071	5.311		3.79%		
MALE	3	810.46	1.237	1.183		0.66%		
FEMALE	21	648.88	4.410	2.649	3.179	2.36%	2.152	0.072
R * M	6	331.51	0.0	1.135		0.0 %	0.803	0.569
R * F	42	367.81	0.0	3.391		0.0 %	0.891	0.659
M * F	63	346.59	0.0	3.843		0.0 %	0.839	0.778
R*M*F	125	412.88	41.874	7.765	9.795	22.44%	3.128	0.0
WITHIN	1579	132.00	131.995	4.695	17.391	70.74%		
ADDITIVE GENETIC VARIANCE			17.640	10.595	6.357			
DOMINANCE GENETIC VARIANCE			0.0	15.373	0.0			
TOTAL PHENOTYPIC VARIANCE			179.516		20.281			
PHENOTYPIC VARIANCE HALF-SIB			9.338		4.626			
PHENOTYPIC VARIANCE FULL-SIB			25.462					
HERITABILITY (INDIVIDUAL)			0.098	0.059		%RESPONSE/i =	1.993	
HERITABILITY (HALF-SIB)			0.472	0.284		%RESPONSE/i =	4.369	
HERITABILITY (FULL-SIB)			0.222	0.208				

TABLE C16. Means and coefficients of variation for volume (VOLM) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

	CLES			GVWS			COMBINED		
GROUP	N	MEAN cm	CV %	N	MEAN cm	CV %	N	MEAN cm	CV %
SEED PARENTS									
415	101	12.42	42.85	42	8.40	35.35	143	11.24	45.24
57	105	15.33	40.41	66	9.79	51.14	171	13.19	48.17
305	100	15.05	48.68	62	10.22	45.49	162	13.20	51.78
72	102	15.78	47.67	53	8.52	46.38	155	13.30	55.41
60	105	15.14	43.34	59	10.04	36.69	164	13.31	46.54
300	104	15.16	45.64	43	9.39	54.69	147	13.47	51.57
323	105	15.09	43.88	48	10.52	52.17	153	13.66	48.49
499	104	14.44	47.00	65	12.70	41.70	169	13.77	45.73
422	102	15.81	39.39	53	9.87	40.93	155	13.78	45.28
303	102	14.83	50.93	60	12.08	38.08	162	13.81	48.75
315	104	16.29	38.53	51	9.77	33.97	155	14.14	44.37
418	103	16.05	41.86	57	10.81	38.98	160	14.18	45.44
310	105	15.84	42.80	54	11.08	45.61	159	14.22	46.60
73	104	16.49	42.00	55	10.85	43.70	159	14.54	46.75
549	107	16.35	46.67	61	11.69	49.38	168	14.66	50.13
110	102	16.95	43.07	52	10.99	44.10	154	14.94	47.80
408	107	16.96	49.38	62	11.70	45.03	169	15.03	51.88
49	100	16.97	49.81	39	10.62	38.58	139	15.19	52.71
193	105	17.53	44.65	61	11.44	54.22	166	15.29	51.19
314	105	18.57	37.03	78	11.57	44.35	183	15.59	45.47
623	103	18.26	43.93	62	12.08	53.23	165	15.94	50.36
439	102	19.74	40.37	68	12.08	42.10	170	16.58	47.37
POLLEN PARENTS									
33	567	16.11	47.21	343	10.74	45.70	910	14.09	51.12
28	570	15.91	48.00	271	10.62	44.32	841	14.20	51.12
62	575	16.06	42.17	284	10.63	45.90	859	14.26	47.06
448	565	16.50	42.61	353	11.28	47.35	918	14.50	47.71
TOTAL	2277	16.14	45.02	1251	10.84	46.01	3528	14.26	49.25

TABLE C17. Combined sites analysis of variance for volume (VOLM).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	22698.99	11.999	11.555		20.35%		
REP/SITE	4	3736.66	6.188	3.673		10.50%		
MALE	4	67.71	0.056	0.080		0.09%		
FEMALE	3	251.80	0.970	0.513	6.905	1.65%	2.479	0.028
S * F	21	69.60	0.127	1.000		0.22%	1.118	0.413
R * F	84	72.75	0.0	0.534		0.0 %	0.761	0.928
M * F	63	117.13	0.556	0.672		0.94%	1.375	0.104
S*M*F	63	85.18	0.0	0.982		0.0 %	0.891	0.703
R/S*M*F	242	95.64	10.356	1.341	22.562	17.57%	3.354	0.0
WITHIN	3010	28.52	28.518	0.735	37.441	48.38%		
ADDITIVE GENETIC VARIANCE			3.880	2.054	13.811			
DOMINANCE GENETIC VARIANCE			2.223	2.687	10.452			
TOTAL PHENOTYPIC VARIANCE			40.764		44.764			
PHENOTYPIC VARIANCE HALF-SIB			1.763		9.309			
PHENOTYPIC VARIANCE FULL-SIB			3.974					
HERITABILITY (INDIVIDUAL)			0.095	-0.050		%RESPONSE/i =	4.261	
HERITABILITY (HALF-SIB)			0.550	0.291		%RESPONSE/i =	10.245	
HERITABILITY (FULL-SIB)			0.628	0.258				

TABLE C17 (Continued). Analysis of variance for trait VOLM on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	4898.09	6.200	4.567		10.98%		
MALE	3	41.64	0.0	0.219		0.0 %		
FEMALE	21	252.88	1.147	0.830	6.633	2.03%	1.872	0.087
R * M	6	233.23	0.445	0.623		0.79%	1.579	0.159
R * F	42	108.77	0.0	0.861		0.0 %	0.736	0.872
M * F	63	174.03	0.977	1.380		1.73%	1.178	0.218
R*M*F	126	147.72	13.193	2.156	22.500	23.37%	4.282	0.0
WITHIN	2013	34.50	34.497	1.087	36.383	61.10%		
ADDITIVE GENETIC VARIANCE			4.586	3.318	13.266			
DOMINANCE GENETIC VARIANCE			3.907	5.521	12.244			
TOTAL PHENOTYPIC VARIANCE			50.258		43.915			
PHENOTYPIC VARIANCE HALF-SIB			2.818		10.398			
PHENOTYPIC VARIANCE FULL-SIB			7.834					
HERITABILITY (INDIVIDUAL)			0.091	0.066			%RESPONSE/i =	4.007
HERITABILITY (HALF-SIB)			0.407	0.294			%RESPONSE/i =	8.462
HERITABILITY (FULL-SIB)			0.271	0.212				

TABLE C17 (Continued). Analysis of variance for trait VOLM on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	2569.94	6.120	4.366		21.14%		
MALE	3	50.66	0.097	0.122		0.33%		
FEMALE	21	66.26	0.892	0.387	8.713	3.08%	2.842	0.046
R * M	6	37.59	0.0	0.189		0.0 %	0.962	0.454
R * F	42	32.09	0.0	0.466		0.0 %	0.821	0.764
M * F	63	30.30	0.0	0.534		0.0 %	0.775	0.866
R*M*F	116	39.08	5.389	1.224	21.413	18.62%	2.376	0.0
WITHIN	997	16.45	16.446	0.736	37.408	56.82%		
ADDITIVE GENETIC VARIANCE			3.569	1.548	17.426			
DOMINANCE GENETIC VARIANCE			0.0	2.134	0.0			
TOTAL PHENOTYPIC VARIANCE			22.824		44.069			
PHENOTYPIC VARIANCE HALF-SIB			1.580		11.596			
PHENOTYPIC VARIANCE FULL-SIB			3.809					
HERITABILITY (INDIVIDUAL)			0.156	0.068			%RESPONSE/i = 6.891	
HERITABILITY (HALF-SIB)			0.565	0.245			%RESPONSE/i = 13.095	
HERITABILITY (FULL-SIB)			0.260	0.203				

TABLE C18. Components of variance and covarjance for traits HT06 and HT12.

FOR VARIABLES	HT06			HT12			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	27.3018	S.E.	11.6735	303.9873	S.E.	113.4067	66.4441
ADDITIVE GENETIC VARIANCE	109.2072	S.E.	46.6941	1215.9492	S.E.	453.6270	265.7764
DOMINANCE GENETIC VARIANCE	0.0	S.E.	42.8132	0.0	S.E.	548.0427	0.0
PHENOTYPIC VARIANCE INDIVIDUAL	868.4045			8981.1406			2107.0273
PHENOTYPIC VARIANCE HALF-SIB	38.5958			461.6140			100.8853
PHENOTYPIC VARIANCE FULL-SIB	88.4654			1108.7012			253.0382
HERITABILTY FOR INDIVIDUAL SELECTION	0.1258	S.E.	0.0538	0.1354	S.E.	0.0505	0.1305
COEFFICIENT OF VARIATION (PI)	27.1366			15.8939			
%RESPONSE /i (INDIVIDUAL)	3.4126			2.1519			
HERITABILTY FOR HALF-SIB SELECTION	0.7074	S.E.	1.2098	0.6585	S.E.	0.9827	0.6825
COEFFICIENT OF VARIATION (PHS)	5.7209			3.6033			
%RESPONSE /i (HALF-SIB)	8.0937	CRy=	5.6956	4.7458	CRx=	3.5874	
GENETIC CORRELATIONS	0.7293	S.E.	0.1322				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0.7545						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	0.7558						
ENVIRONMENTAL CORRELATIONS	0.7583						

TABLE C19. Components of variance and covariance for traits HT06 and DM12.

FOR VARIABLES	HT06			DM12			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	27.3018	S.E.	11.6735	6.5144	S.E.	2.3512	6.8592
ADDITIVE GENETIC VARIANCE	109.2072	S.E.	46.6941	26.0576	S.E.	9.4048	27.4366
DOMINANCE GENETIC VARIANCE	0.0	S.E.	42.8132	0.0	S.E.	8.9483	0.0
PHENOTYPIC VARIANCE INDIVIDUAL	868.4045			157.2119			245.3063
PHENOTYPIC VARIANCE HALF-SIB	38.5958			8.8543			10.5249
PHENOTYPIC VARIANCE FULL-SIB	88.4654			15.8838			22.8709
HERITABILTY FOR INDIVIDUAL SELECTION	0.1258	S.E.	0.0538	0.1657	S.E.	0.0598	0.1444
COEFFICIENT OF VARIATION (PI)	27.1366			16.0574			
%RESPONSE /i (INDIVIDUAL)	3.4126			2.6615			
HERITABILTY FOR HALF-SIB SELECTION	0.7074	S.E.	1.2098	0.7357	S.E.	1.0622	0.7214
COEFFICIENT OF VARIATION (PHS)	5.7209			3.8107			
%RESPONSE /i (HALF-SIB)	8.0937	CRy=	4.2454	5.6074	CRx=	2.8279	
GENETIC CORRELATIONS	0.5143	S.E.	0.2043				
PHENOTYPIC CORRELATIONS.INDIVIDUAL	0.6639						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	0.5693						
ENVIRONMENTAL CORRELATIONS	0.6904						

TABLE C20. Components of variance and covariance for traits HT12 and DM12.

FOR VARIABLES	HT12			DM12			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	303.9873	S.E.	113.4067	6.5144	S.E.	2.3512	20.0828
ADDITIVE GENETIC VARIANCE	1215.9492	S.E.	453.6270	26.0576	S.E.	9.4048	80.3307
DOMINANCE GENETIC VARIANCE	0.0	S.E.	548.0427	0.0	S.E.	8.9483	0.0
PHENOTYPIC VARIANCE INDIVIDUAL	8981.1406			157.2119			964.9590
PHENOTYPIC VARIANCE HALF-SIB	461.6140			8.8543			37.1930
PHENOTYPIC VARIANCE FULL-SIB	1108.7012			15.8838			85.5430
HERITABILTY FOR INDIVIDUAL SELECTION	0.1354	S.E.	0.0505	0.1657	S.E.	0.0598	0.1498
COEFFICIENT OF VARIATION (PI)	15.8939			16.0574			
%RESPONSE /i (INDIVIDUAL)	2.1519			2.6615			
HERITABILTY FOR HALF-SIB SELECTION	0.6585	S.E.	0.9827	0.7357	S.E.	1.0622	0.6961
COEFFICIENT OF VARIATION (PHS)	3.6033			3.8107			
%RESPONSE /i (HALF-SIB)	4.7458	CRy=	2.2638	5.6074	CRx=	2.3941	
GENETIC CORRELATIONS	0.4513	S.E.	0.2066				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0.8121						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	0.5818						
ENVIRONMENTAL CORRELATIONS	0.8766						

TABLE C21. Components of variance and covariance for traits HT06 and VOLM.

FOR VARIABLES	HT06			VOLM			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	17.2734	S.E.	9.7749	97.0063	S.E.	51.3499	27.9492
ADDITIVE GENETIC VARIANCE	69.0936	S.E.	39.0998	388.0251	S.E.	205.3995	111.7970
DOMINANCE GENETIC VARIANCE	43.8912	S.E.	40.1620	222.2556	S.E.	268.6882	80.8400
PHENOTYPIC VARIANCE INDIVIDUAL	778.5940			4076.4172			1425.1563
PHENOTYPIC VARIANCE HALF-SIB	31.8183			176.2940			55.5638
PHENOTYPIC VARIANCE FULL-SIB	71.1595			397.4338			129.0417
HERITABILTY FOR INDIVIDUAL SELECTION	0.0887	S.E.	0.0502	0.0952	S.E.	0.0504	0.0919
COEFFICIENT OF VARIATION (PI)	24.5405			44.7636			
%RESPONSE /i. (INDIVIDUAL)	2.1778			4.2609			
HERITABILITY FOR HALF-SIB SELECTION	0.5429	S.E.	1.2288	0.5503	S.E.	1.1651	0.5466
COEFFICIENT OF VARIATION (PHS)	4.9610			9.3090			
%RESPONSE /i (HALF-SIB)	5.3864	CRy=	3.7026	10.2446	CRx=	6.9478	
GENETIC CORRELATIONS	0.6828	S.E.	0.2066				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0.8000						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	0.7419						
ENVIRONMENTAL CORRELATIONS	0.8119						

APPENDIX D: Tables of means and analyses of variance and covariance for form traits.

TABLE D1. Means and coefficients of variation for branch number (BN) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

	CLES			GVWS			COMBINED		
GROUP	N	MEAN cm	CV %	N	MEAN cm	CV %	N	MEAN cm	CV %
SEED PARENTS									
418	103	4.68	18.61	57	5.08	20.02	160	4.82	19.52
300	104	5.04	23.41	43	4.71	26.74	147	4.94	24.45
415	101	4.85	20.41	42	5.18	23.05	143	4.94	21.44
57	105	4.83	23.28	66	5.37	25.68	171	5.04	24.87
323	105	4.96	21.68	48	5.51	21.22	153	5.13	22.03
49	100	5.01	16.03	39	5.59	21.61	139	5.17	18.69
549	107	5.05	16.92	61	5.48	16.81	168	5.21	17.31
310	105	4.98	22.35	54	5.77	22.95	159	5.25	23.69
315	104	5.08	24.26	51	5.62	21.11	155	5.26	23.58
193	105	5.06	28.44	61	5.63	21.68	166	5.27	26.32
72	102	5.10	20.70	53	5.65	19.60	155	5.29	20.84
499	104	5.05	21.67	65	5.68	20.49	169	5.29	21.93
60	105	5.08	27.30	59	5.78	23.52	164	5.33	26.51
408	107	5.20	21.71	62	5.80	19.02	169	5.42	21.28
305	100	5.07	18.54	62	6.02	18.97	162	5.43	20.58
73	104	5.21	20.84	55	5.90	38.75	159	5.45	29.96
110	102	5.31	17.98	52	5.88	19.38	154	5.50	19.14
623	103	5.53	18.86	62	5.85	15.91	165	5.65	17.89
314	105	5.27	18.29	78	6.20	19.08	183	5.66	20.40
439	102	5.35	20.12	68	6.15	19.41	170	5.67	20.97
422	102	5.61	18.67	53	5.97	20.47	155	5.74	19.53
303	102	5.58	19.69	60	6.63	16.47	162	5.97	20.19
POLLEN PARENTS									
33	567	5.00	20.81	343	5.67	19.84	910	5.25	21.32
28	570	5.10	22.08	271	5.66	28.33	841	5.28	25.10
448	565	5.08	20.87	353	5.78	22.32	918	5.35	22.48
62	575	5.34	21.52	284	5.83	19.46	859	5.50	21.20
TOTAL	2277	5.13	21.48	1251	5.73	22.51	3528	5.34	22.59

TABLE D2. Combined sites analysis of variance for branch number (BN).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	295.12	0.164	0.150		10.47%		
REP/SITE	4	31.34	0.052	0.031		3.31%		
MALE	3	12.59	0.013	0.009		0.82%		
FEMALE	21	12.11	0.064	0.023	4.723	4.06%	5.976	0.011
S * F	21	2.64	0.0	1.000		0.0 %	0.928	0.561
R * F	84	2.26	0.002	0.015		0.11%	1.065	0.352
M * F	63	2.10	0.0	0.016		0.0 %	0.773	0.845
S*M*F	63	2.71	0.004	0.029		0.24%	1.279	0.097
R/S*M*F	242	2.12	0.155	0.030	7.367	9.89%	1.903	0.0
WITHIN	3010	1.11	1.114	0.029	19.744	71.01%		
ADDITIVE GENETIC VARIANCE			0.255	0.093	9.445			
DOMINANCE GENETIC VARIANCE			0.0	0.063	0.0			
TOTAL PHENOTYPIC VARIANCE			1.352		21.757			
PHENOTYPIC VARIANCE HALF-SIB			0.078		5.213			
PHENOTYPIC VARIANCE FULL-SIB			0.131					
HERITABILITY (INDIVIDUAL)			0.188	0.069		%RESPONSE/i =	4.100	
HERITABILITY (HALF-SIB)			0.821	0.299		%RESPONSE/i =	8.557	
HERITABILITY (FULL-SIB)			0.971	0.354				

TABLE D2 (Continued). Analysis of variance for branch number on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	371706.75	480.552	346.437		3.86%		
MALE	3	124632.94	203.770	138.897		1.64%		
FEMALE	21	56334.34	338.218	172.189	3.585	2.71%	2.631	0.016
R * M	6	7909.76	0.0	25.217		0.0 %	0.370	0.897
R * F	42	20576.62	0.0	149.268		0.0 %	0.963	0.542
M * F	63	22197.26	28.275	182.985		0.23%	1.039	0.421
R*M*F	126	21361.35	1312.530	313.336	7.062	10.53%	2.116	0.0
WITHIN	2013	10097.18	10097.188	318.110	19.586	81.03%		
ADDITIVE GENETIC VARIANCE			1352.873	688.757	7.169			
DOMINANCE GENETIC VARIANCE			113.099	731.940	2.073			
TOTAL PHENOTYPIC VARIANCE			11979.973		21.334			
PHENOTYPIC VARIANCE HALF-SIB			551.676		4.578			
PHENOTYPIC VARIANCE FULL-SIB			1396.303					
HERITABILITY (INDIVIDUAL)			0.113	0.057		%RESPONSE/I =	2.409	
HERITABILITY (HALF-SIB)			0.613	0.312		%RESPONSE/I =	5.613	
HERITABILITY (FULL-SIB)			0.408	0.247				

TABLE D2 (Continued). Analysis of variance for branch number on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	319322.31	744.679	542.608		4.35%		
MALE	3	16051.82	23.288	38.349		0.14%		
FEMALE	21	86033.81	1011.551	466.192	5.546	5.91%	2.871	0.004
R * M	6	6980.35	0.0	43.423		0.0 %	0.332	0.919
R * F	42	25771.42	133.086	335.895		0.78%	1.227	0.197
M * F	63	25192.54	135.298	377.328		0.79%	1.200	0.198
R*M*F	116	20995.94	1848.119	665.913	7.496	10.79%	1.587	0.000
WITHIN	997	13233.30	13233.309	592.107	20.059	77.26%		
ADDITIVE GENETIC VARIANCE			4046.205	1864.769	11.091			
DOMINANCE GENETIC VARIANCE			541.191	1509.311	4.056			
TOTAL PHENOTYPIC VARIANCE			16384.645		22.319			
PHENOTYPIC VARIANCE HALF-SIB			1457.210		6.656			
PHENOTYPIC VARIANCE FULL-SIB			2684.957					
HERITABILITY (INDIVIDUAL)			0.247	0.114		%RESPONSE/i =	5.512	
HERITABILITY (HALF-SIB)			0.694	0.320		%RESPONSE/i =	9.241	
HERITABILITY (FULL-SIB)			0.436	0.347				

TABLE D3. Means and coefficients of variation for branch angle (BA) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

GROUP	CLES N	CLES MEAN cm	CLES CV %	GVWS N	GVWS MEAN cm	GVWS CV %	COMBINED N	COMBINED MEAN cm	COMBINED CV %
SEED PARENTS									
418	103	57.61	10.63	57	62.59	11.18	160	59.38	11.55
323	105	60.63	13.26	48	64.40	12.15	153	61.81	13.16
439	102	61.70	9.74	68	62.52	9.10	170	62.03	9.48
415	101	61.25	10.48	42	64.74	9.24	143	62.27	10.39
315	104	61.87	11.25	51	65.84	10.66	155	63.17	11.41
314	105	62.02	9.48	78	65.27	10.59	183	63.41	10.29
305	100	63.23	10.99	62	65.23	10.68	162	63.99	10.95
49	100	63.48	9.79	39	66.07	11.65	139	64.21	10.49
300	104	63.86	9.37	43	65.39	11.93	147	64.31	10.23
303	102	63.06	10.42	60	67.43	9.05	162	64.68	10.40
57	105	64.03	9.49	66	68.93	10.43	171	65.92	10.52
422	102	64.61	10.43	53	69.38	6.96	155	66.24	9.88
499	104	65.96	9.30	65	67.52	7.73	169	66.56	8.76
408	107	65.44	8.94	62	68.55	8.73	169	66.58	9.12
73	104	66.45	9.84	55	68.44	9.63	159	67.14	9.84
60	105	66.17	9.36	59	69.13	8.67	164	67.24	9.32
110	102	66.91	9.68	52	68.22	13.29	154	67.35	11.06
623	103	67.20	9.79	62	68.81	7.57	165	67.80	9.05
549	107	68.71	8.63	61	68.69	8.54	168	68.70	8.57
72	102	70.65	8.23	53	70.94	9.47	155	70.75	8.65
310	105	70.28	7.96	54	72.25	7.18	159	70.95	7.78
193	105	70.50	8.22	61	72.53	8.49	166	71.24	8.41
POLLEN PARENTS									
33	567	63.43	11.96	343	66.81	10.04	910	64.71	11.50
28	570	64.68	10.93	271	66.03	11.46	841	65.12	11.14
448	565	64.64	9.89	353	67.62	10.03	918	65.79	10.24
62	575	66.49	10.61	284	69.27	9.69	859	67.41	10.48
TOTAL	2277	64.82	11.01	1251	67.43	10.40	3528	65.74	10.95

TABLE D4. Combined sites analysis of variance for branch angle (BA).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	5509.33	2.107	2.896		3.87%		
REP/SITE	4	2214.95	3.641	2.177		6.70%		
MALE	3	1306.29	1.301	0.941		2.39%		
FEMALE	21	1559.09	8.851	2.876	4.525	16.27%	11.663	0.000
S * F	21	90.09	0.359	1.000		0.66%	1.383	0.187
R * F	84	64.13	0.370	0.413		0.68%	1.218	0.126
M * F	63	97.24	0.996	0.502		1.83%	1.812	0.010
S*M*F	63	53.65	0.060	0.601		0.11%	1.019	0.447
R/S*M*F	242	52.65	2.942	0.747	2.609	5.41%	1.568	0.000
WITHIN	3010	33.58	33.583	0.865	8.815	61.75%		
ADDITIVE GENETIC VARIANCE			35.404	11.502	9.050			
DOMINANCE GENETIC VARIANCE			3.983	2.009	3.036			
TOTAL PHENOTYPIC VARIANCE			48.637		10.608			
PHENOTYPIC VARIANCE HALF-SIB			9.659		4.727			
PHENOTYPIC VARIANCE FULL-SIB			12.491					
HERITABILITY (INDIVIDUAL)			0.728	0.236		%RESPONSE/i =	7.722	
HERITABILITY (HALF-SIB)			0.916	0.298		%RESPONSE/i =	8.664	
HERITABILITY (FULL-SIB)			1.497	0.460				

TABLE D4 (Continued). Analysis of variance for branch angle on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	2238.48	2.909	2.086		5.50%		
MALE	3	919.40	1.539	1.022		2.91%		
FEMALE	21	1205.20	10.742	3.440	5.056	20.29%	12.887	0.0
R * M	6	19.93	0.0	0.065		0.0 %	0.341	0.914
R * F	42	69.75	0.320	0.482		0.60%	1.192	0.228
M * F	63	82.28	0.910	0.627		1.72%	1.406	0.054
R*M*F	126	58.51	2.902	0.861	2.628	5.48%	1.741	0.000
WITHIN	2013	33.61	33.612	1.059	8.944	63.50%		
ADDITIVE GENETIC VARIANCE			42.968	13.762	10.113			
DOMINANCE GENETIC VARIANCE			3.640	2.503	2.944			
TOTAL PHENOTYPIC VARIANCE			50.024		10.912			
PHENOTYPIC VARIANCE HALF-SIB			11.641		5.264			
PHENOTYPIC VARIANCE FULL-SIB			15.454					
HERITABILITY (INDIVIDUAL)			0.859	0.275		%RESPONSE/i =	9.373	
HERITABILITY (HALF-SIB)			0.923	0.296		%RESPONSE/i =	9.715	
HERITABILITY (FULL-SIB)			0.854	0.445				

TABLE D4 (Continued). Analysis of variance for branch angle on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	2329.69	5.294	3.960		10.26%		
MALE	3	557.17	1.365	1.147		2.64%		
FEMALE	21	421.69	6.002	2.213	3.633	11.63%	5.186	0.000
R * M	6	112.38	0.595	0.549		1.15%	2.428	0.030
R * F	42	60.53	0.567	0.780		1.10%	1.308	0.133
M * F	63	67.06	1.224	0.960		2.37%	1.449	0.043
R*M*F	116	46.28	3.039	1.478	2.585	5.89%	1.381	0.007
WITHIN	997	33.52	33.523	1.500	8.587	64.96%		
ADDITIVE GENETIC VARIANCE			24.006	8.854	7.266			
DOMINANCE GENETIC VARIANCE			4.896	3.839	3.281			
TOTAL PHENOTYPIC VARIANCE			46.314		10.093			
PHENOTYPIC VARIANCE HALF-SIB			7.298		4.006			
PHENOTYPIC VARIANCE FULL-SIB			11.930					
HERITABILITY (INDIVIDUAL)			0.518	0.191		%RESPONSE/i =	5.231	
HERITABILITY (HALF-SIB)			0.822	0.303		%RESPONSE/i =	6.589	
HERITABILITY (FULL-SIB)			0.720	0.371				

TABLE D5. Means and coefficients of variation for branch thickness (BT) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

GROUP	CLES N	CLES MEAN mm	CLES CV %	GVWS N	GVWS MEAN mm	GVWS CV %	COMBINED N	COMBINED MEAN mm	COMBINED CV %
SEED PARENTS									
300	104	18.68	16.84	43	17.80	17.76	147	18.42	17.18
315	104	19.24	14.89	51	17.60	14.99	155	18.70	15.45
60	105	19.08	16.00	59	18.26	12.74	164	18.79	15.09
499	104	18.93	17.09	65	18.99	15.63	169	18.95	16.50
72	102	19.67	17.52	53	17.83	15.47	155	19.05	17.52
415	101	19.34	13.68	42	18.45	15.04	143	19.08	14.18
314	105	20.05	15.34	78	17.83	15.11	183	19.10	16.28
303	102	19.58	17.79	60	18.44	14.77	162	19.16	17.02
305	100	19.64	16.79	62	18.67	18.25	162	19.27	17.45
57	105	20.15	15.15	66	18.30	12.97	171	19.44	15.15
193	105	20.15	16.60	61	18.24	14.12	166	19.44	16.51
310	105	19.88	18.73	54	18.71	14.98	159	19.48	17.83
408	107	20.19	15.84	62	18.38	14.62	169	19.[illegible]	16.07
422	102	20.42	14.34	53	17.95	16.10	155	19.[illegible]	16.01
73	104	20.28	14.85	55	18.35	12.54	159	19.62	14.93
110	102	20.21	16.07	52	18.80	15.08	154	19.73	16.09
323	105	20.14	17.10	48	19.16	17.25	153	19.83	17.25
549	107	20.53	16.89	61	18.93	20.52	168	19.95	18.51
623	103	20.37	17.02	62	19.28	18.15	165	19.96	17.58
439	102	20.77	17.01	68	18.78	13.75	170	19.97	16.65
49	100	20.44	19.80	39	19.40	17.12	139	20.15	19.23
418	103	21.15	17.19	57	19.11	13.36	160	20.42	16.77
POLLEN PARENTS									
62	575	19.34	16.37	284	17.75	14.71	859	18.81	16.40
28	570	19.92	17.14	271	18.59	16.25	841	19.49	17.19
448	565	20.23	16.71	353	18.85	15.95	918	19.70	16.80
33	567	20.32	16.34	343	18.72	15.05	910	19.72	16.40
TOTAL	2277	19.95	16.75	1251	18.51	15.67	3528	19.44	16.80

TABLE D6. Combined sites analysis of variance for branch thickness (BT).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	1679.71	0.700	0.877		5.99%		
REP/SITE	4	612.85	1.011	0.602		8.65%		
MALE	3	181.68	0.195	0.131		1.67%		
FEMALE	21	40.99	0.130	0.087	1.858	1.12%	1.991	0.065
S * F	21	13.86	0.016	1.000		0.14%	1.040	0.469
R * F	84	18.00	0.0	0.125		0.0 %	0.899	0.712
M * F	63	22.08	0.140	0.127		1.20%	1.438	0.076
S*M*F	63	15.36	0.0	0.185		0.0 %	0.767	0.895
R/S*M*F	242	20.03	1.923	0.281	7.134	16.45%	2.647	0.0
WITHIN	3010	7.57	7.567	0.195	14.152	64.75%		
ADDITIVE GENETIC VARIANCE			0.522	0.349	3.715			
DOMINANCE GENETIC VARIANCE			0.562	0.506	3.856			
TOTAL PHENOTYPIC VARIANCE			9.976		16.250			
PHENOTYPIC VARIANCE HALF-SIB			0.298		2.808			
PHENOTYPIC VARIANCE FULL-SIB			0.967					
HERITABILITY (INDIVIDUAL)			0.052	0.035		%RESPONSE/I =	0.849	
HERITABILITY (HALF-SIB)			0.438	0.293		%RESPONSE/I =	2.458	
HERITABILITY (FULL-SIB)			0.415	0.181				

TABLE D6 (Continued). Analysis of variance for branch thickness on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	18961.08	20.836	17.861		1.81%		
MALE	3	11281.43	13.388	13.012		1.16%		
FEMALE	21	3986.85	18.481	13.522	2.155	1.60%	1.907	0.109
R * M	6	3795.84	4.934	10.182		0.43%	1.337	0.246
R * F	42	2210.16	0.0	17.133		0.0 %	0.778	0.823
M * F	63	2720.07	0.0	23.021		0.0 %	0.958	0.568
R*M*F	126	2839.88	230.130	41.486	7.604	19.97%	3.284	0.0
WITHIN	2013	864.89	864.899	27.248	14.742	75.03%		
ADDITIVE GENETIC VARIANCE			73.923	54.088	4.310			
DOMINANCE GENETIC VARIANCE			0.0	92.085	0.0			
TOTAL PHENOTYPIC VARIANCE			1131.832		16.864			
PHENOTYPIC VARIANCE HALF-SIB			45.920		3.397			
PHENOTYPIC VARIANCE FULL-SIB			141.687					
HERITABILITY (INDIVIDUAL)			0.065	0.048		%RESPONSE/i =	1.101	
HERITABILITY (HALF-SIB)			0.402	0.294		%RESPONSE/i =	2.734	
HERITABILITY (FULL-SIB)			0.225	0.191				

TABLE D6 (Continued). Analysis of variance for branch thickness on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	102348.25	243.421	173.853		25.70%		
MALE	3	8377.05	24.534	17.102		2.59%		
FEMALE	21	1484.87	6.470	10.015	1.374	0.68%	1.180	0.348
R * M	6	968.52	0.0	4.906		0.0 %	0.885	0.508
R * F	42	1301.76	2.238	17.045		0.24%	1.190	0.233
M * F	63	1050.75	0.0	16.894		0.0 %	0.961	0.563
R*M*F	116	1093.76	132.237	34.385	6.214	13.96%	2.032	0.0
WITHIN	997	538.33	538.333	24.087	12.537	56.83%		
ADDITIVE GENETIC VARIANCE			25.880	40.059	2.749			
DOMINANCE GENETIC VARIANCE			0.0	67.577	0.0			
TOTAL PHENOTYPIC VARIANCE			703.813		14.335			
PHENOTYPIC VARIANCE HALF-SIB			26.449		2.779			
PHENOTYPIC VARIANCE FULL-SIB			109.917					
HERITABILITY (INDIVIDUAL)			0.037	0.057		%RESPONSE/I =	0.527	
HERITABILITY (HALF-SIB)			0.245	0.379		%RESPONSE/I =	1.360	
HERITABILITY (FULL-SIB)			0.282	0.182				

TABLE D7. Means and coefficients of variation for proportional branch thickness (BTT) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

	CLES			GVWS			COMBINED		
GROUP	N	MEAN %	CV %	N	MEAN %	CV %	N	MEAN %	CV %
SEED PARENTS									
314	105	24.65	11.65	78	26.97	13.06	183	25.64	13.10
439	102	25.05	13.49	68	27.90	9.24	170	26.19	12.90
300	104	25.24	14.23	43	28.77	14.86	147	26.27	15.67
315	104	25.63	12.36	51	27.82	14.59	155	26.35	13.75
193	105	25.44	11.99	61	28.27	10.29	166	26.48	12.42
60	105	25.72	11.64	59	28.68	9.36	164	26.78	12.00
310	105	25.87	13.07	54	28.65	11.43	159	26.82	13.38
110	102	25.87	12.33	52	28.87	10.96	154	26.88	12.93
49	100	26.00	11.69	39	29.16	9.64	139	26.89	12.25
499	104	26.16	10.58	65	28.38	9.01	169	27.01	10.71
72	102	25.70	9.99	53	29.88	11.18	155	27.13	12.79
303	102	26.76	12.66	60	28.19	11.10	162	27.29	12.30
623	103	25.84	13.29	62	29.95	11.32	165	27.38	14.42
73	104	26.71	10.71	55	28.69	10.31	159	27.39	11.09
408	107	27.04	11.14	62	28.32	11.79	169	27.51	11.58
549	107	27.10	11.22	61	28.68	8.79	168	27.67	10.68
422	102	27.08	11.49	53	28.86	9.42	155	27.69	11.17
305	100	26.86	10.02	62	30.45	13.07	162	28.23	13.02
323	105	27.43	10.95	48	30.29	13.21	153	28.32	12.68
415	101	27.48	10.55	42	31.16	12.36	143	28.56	12.64
57	105	27.53	10.71	66	30.47	11.18	171	28.67	11.99
418	103	28.80	12.50	57	29.81	11.89	160	29.16	12.35
POLLEN PARENT									
62	575	25.27	11.74	284	28.00	12.34	859	26.17	12.95
28	570	26.43	12.76	271	28.73	12.04	841	27.17	13.12
448	565	26.82	12.72	353	29.33	11.40	918	27.78	12.95
33	567	26.95	10.78	343	29.49	11.02	910	27.91	11.75
TOTAL	2277	26.36	12.28	1251	28.94	11.80	3528	27.28	12.92

TABLE D8. Combined sites analysis of variance for branch thickness expressed as proportion (%) of stem diameter (BTT).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	5384.76	2.813	2.743		19.49%		
REP/SITE	4	929.63	1.535	0.914		10.63%		
MALE	3	470.51	0.525	0.338		3.64%		
FEMALE	21	138.14	0.659	0.261	2.976	4.56%	4.408	0.001
S * F	21	26.13	0.045	1.000		0.31%	1.115	0.367
R * F	84	22.20	0.212	0.139		1.47%	1.404	0.025
M * F	63	22.27	0.082	0.128		0.57%	1.305	0.147
S*M*F	63	17.06	0.072	0.189		0.50%	1.078	0.338
R/S*M*F	242	15.82	1.343	0.223	4.248	9.30%	2.223	0.0
WITHIN	3010	7.12	7.116	0.183	9.780	49.29%		
ADDITIVE GENETIC VARIANCE			2.636	1.046	5.952			
DOMINANCE GENETIC VARIANCE			0.328	0.513	2.100			
TOTAL PHENOTYPIC VARIANCE			10.087		11.644			
PHENOTYPIC VARIANCE HALF-SIB			0.841		3.363			
PHENOTYPIC VARIANCE FULL-SIB			1.693					
HERITABILITY (INDIVIDUAL)			0.261	0.104		%RESPONSE/i =	3.042	
HERITABILITY (HALF-SIB)			0.783	0.311		%RESPONSE/i =	5.267	
HERITABILITY (FULL-SIB)			0.827	0.309				

TABLE D8 (Continued). Analysis of variance for branch thickness (proportional) on site CLES.

SOURCE	D.F.	MEAN, SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	65369.38	83.482	60.919		7.62%		
MALE	3	33180.56	55.218	36.896		5.04%		
FEMALE	21	10291.68	73.989	30.018	3.263	6.75%	3.898	0.000
R * M	6	1481.50	0.0	4.088		0.0 %	0.813	0.562
R * F	42	2364.90	15.446	16.064		1.41%	1.298	0.137
M * F	63	2098.00	10.255	16.761		0.94%	1.151	0.251
R*M*F	126	1822.63	127.291	26.682	4.280	11.62%	2.496	0.0
WITHIN	2013	730.22	730.223	23.005	10.251	66.63%		
ADDITIVE GENETIC VARIANCE			295.954	120.073	6.526			
DOMINANCE GENETIC VARIANCE			41.022	67.044	2.430			
TOTAL PHENOTYPIC VARIANCE			1012.421		12.070			
PHENOTYPIC VARIANCE HALF-SIB			99.306		3.780			
PHENOTYPIC VARIANCE FULL-SIB			209.943					
HERITABILITY (INDIVIDUAL)			0.292	0.119		%RESPONSE/i =	3.528	
HERITABILITY (HALF-SIB)			0.745	0.302		%RESPONSE/i =	5.633	
HERITABILITY (FULL-SIB)			0.664	0.286				

TABLE D8 (Continued). Analysis of variance for branch thickness (proportional) on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	128165.75	298.515	217.737		23.36%		
MALE	3	10656.80	22.864	22.275		1.79%		
FEMALE	21	5948.59	60.861	32.488	2.695	4.76%	2.320	0.012
R * M	6	3197.89	15.877	15.616		1.24%	2.421	0.031
R * F	42	2091.50	31.409	26.089		2.46%	1.584	0.029
M * F	63	1793.23	20.144	25.955		1.58%	1.358	0.078
R*M*F	116	1320.66	153.956	41.562	4.287	12.05%	1.959	0.0
WITHIN	997	674.00	674.008	30.157	8.970	52.75%		
ADDITIVE GENETIC VARIANCE			243.446	129.953	5.391			
DOMINANCE GENETIC VARIANCE			80.578	103.822	3.101			
TOTAL PHENOTYPIC VARIANCE			979.119		10.811			
PHENOTYPIC VARIANCE HALF-SIB			99.177		3.441			
PHENOTYPIC VARIANCE FULL-SIB			199.153					
HERITABILITY (INDIVIDUAL)			0.249	0.133		%RESPONSE/i =	2.688	
HERITABILITY (HALF-SIB)			0.614	0.328		%RESPONSE/i =	4.223	
HERITABILITY (FULL-SIB)			0.522	0.326				

TABLE D9. Means and coefficients of variation for branch length (BL) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

GROUP	CLES N	MEAN cm	CV %	GVWS N	MEAN cm	CV %	COMBINED N	MEAN cm	CV %
SEED PARENTS									
72	102	152.04	15.05	53	126.88	11.98	155	143.43	16.57
303	102	157.23	16.27	60	139.33	14.96	162	150.60	16.86
300	104	157.39	15.38	43	134.37	13.93	147	150.66	16.59
110	102	158.93	14.90	52	137.23	14.42	154	151.60	16.25
323	105	158.89	17.03	48	136.65	13.97	153	151.91	17.68
415	101	159.09	13.06	42	135.81	15.26	143	152.25	15.28
57	105	162.96	14.33	66	135.77	13.37	171	152.47	16.54
499	104	156.91	17.15	65	146.02	14.44	169	152.72	16.58
315	104	162.36	13.21	51	134.43	14.24	155	153.17	15.99
305	100	165.23	15.85	62	140.42	14.08	162	155.73	17.19
549	107	163.99	15.86	61	141.74	15.11	168	155.91	17.08
314	105	169.85	14.90	78	137.73	14.43	183	156.16	17.96
193	105	167.75	15.53	61	138.09	14.48	166	156.85	17.79
422	102	168.92	12.30	53	131.23	12.93	155	157.06	16.33
439	102	171.43	15.68	68	138.04	12.62	170	158.07	18.13
623	103	168.72	15.85	62	142.33	13.77	165	158.80	17.27
60	105	167.11	14.75	59	144.40	13.96	164	158.94	16.06
310	105	167.60	16.41	54	143.77	12.94	159	159.50	17.08
73	104	170.00	14.94	55	139.88	12.22	159	159.58	16.90
408	107	171.65	15.25	62	144.50	12.71	169	161.69	16.68
418	103	173.20	13.02	57	148.25	13.58	160	164.31	15.06
49	100	171.63	18.30	39	149.00	11.70	139	165.28	18.10
POLLEN PARENTS									
33	567	161.87	15.75	343	137.42	14.12	910	152.66	17.17
28	570	162.30	15.76	271	140.53	14.33	841	155.28	16.76
448	565	167.26	15.50	353	141.76	13.69	918	157.45	16.94
62	575	167.31	15.28	284	138.54	14.14	859	157.80	17.32
TOTAL	2277	164.69	15.64	1251	139.57	14.09	3528	155.78	17.10

TABLE D10. Combined sites analysis of variance for branch length (BL).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	509219.50	306.048	257.536		33.10%		
REP/SITE	4	15388.20	24.961	15.142		2.70%		
MALE	3	4846.86	3.035	3.685		0.33%		
FEMALE	21	4185.65	15.921	8.239	2.561	1.72%	2.586	0.011
S * F	21	1000.81	6.687	1.000		0.72%	1.790	0.185
R * F	84	995.86	0.0	7.374		0.0 %	0.742	0.944
M * F	63	1522.78	13.926	8.351		1.51%	1.682	0.020
S*M*F	63	905.10	0.0	11.370		0.0 %	0.674	0.968
R/S*M*F	242	1342.00	144.096	18.815	7.706	15.58%	3.289	0.0
WITHIN	3010	408.01	408.013	10.514	12.966	44.13%		
ADDITIVE GENETIC VARIANCE			63.683	32.956	5.123			
DOMINANCE GENETIC VARIANCE			55.704	33.406	4.791			
TOTAL PHENOTYPIC VARIANCE			593.661		15.640			
PHENOTYPIC VARIANCE HALF-SIB			30.805		3.563			
PHENOTYPIC VARIANCE FULL-SIB			66.457					
HERITABILITY (INDIVIDUAL)			0.107	0.056		%RESPONSE/i =	1.678	
HERITABILITY (HALF-SIB)			0.517	0.267		%RESPONSE/i =	3.683	
HERITABILITY (FULL-SIB)			0.689	0.248				

TABLE D10 (Continued). Analysis of variance for branch length on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	13222.12	15.655	12.393		2.27%		
MALE	3	5150.12	5.922	5.995		0.86%		
FEMALE	21	3752.12	23.465	11.747	2.941	3.40%	2.810	0.030
R * M	6	1868.04	0.0	5.086		0.0 %	0.970	0.448
R * F	42	1412.31	0.0	11.191		0.0 %	0.734	0.875
M * F	63	1848.53	0.0	15.626		0.0 %	0.960	0.564
R*M*F	126	1925.33	168.824	28.098	7.890	24.45%	4.041	0.0
WITHIN	2013	476.48	476.489	15.011	13.255	68.02%		
ADDITIVE GENETIC VARIANCE			93.861	46.988	5.883			
DOMINANCE GENETIC VARIANCE			0.0	62.504	0.0			
TOTAL PHENOTYPIC VARIANCE			674.700		15.772			
PHENOTYPIC VARIANCE HALF-SIB			42.068		3.938			
PHENOTYPIC VARIANCE FULL-SIB			103.840					
HERITABILITY (INDIVIDUAL)			0.139	0.070		%RESPONSE/i =	2.194	
HERITABILITY (HALF-SIB)			0.558	0.279		%RESPONSE/i =	4.394	
HERITABILITY (FULL-SIB)			0.283	0.226				

TABLE D10 (Continued). Analysis of variance for branch length on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	18467.32	43.637	31.380		9.93%		
MALE	3	1311.32	2.929	2.902		0.67%		
FEMALE	21	1324.88	18.720	7.564	3.100	4.26%	3.227	0.030
R * M	6	659.90	0.0	3.328		0.0 %	0.932	0.475
R * F	42	516.35	0.0	7.852		0.0 %	0.729	0.878
M * F	63	602.60	0.0	10.159		0.0 %	0.851	0.758
R*M*F	116	708.38	104.428	22.145	7.322	23.76%	2.626	0.0
WITHIN	997	269.75	269.757	12.070	11.767	61.38%		
ADDITIVE GENETIC VARIANCE			74.881	30.255	6.200			
DOMINANCE GENETIC VARIANCE			0.0	40.634	0.0			
TOTAL PHENOTYPIC VARIANCE			395.833		14.254			
PHENOTYPIC VARIANCE HALF-SIB			31.191		4.001			
PHENOTYPIC VARIANCE FULL-SIB			72.757					
HERITABILITY (INDIVIDUAL)			0.189	0.076		%RESPONSE/i =	2.697	
HERITABILITY (HALF-SIB)			0.600	0.242		%RESPONSE/i =	4.803	
HERITABILITY (FULL-SIB)			0.298	0.208				

TABLE D11. Means and coefficients of variation for proportional branch length (BLT) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

	CLES			GVWS			COMBINED		
GROUP	N	MEAN %	CV %	N	MEAN %	CV %	N	MEAN %	CV %
SEED PARENTS									
110	102	37.76	10.89	52	36.04	12.16	154	37.18	11.48
499	104	37.94	9.49	65	36.40	13.13	169	37.35	11.11
315	104	37.97	13.50	51	36.78	13.31	155	37.58	13.48
623	103	38.58	11.90	62	36.49	9.87	165	37.79	11.52
57	105	38.41	10.14	66	36.83	11.32	171	37.80	10.75
323	105	38.78	11.18	48	37.01	12.77	153	38.23	11.83
303	102	39.52	9.47	60	36.47	15.85	162	38.39	12.55
549	107	38.83	11.42	61	37.67	13.92	168	38.41	12.40
314	105	39.51	11.75	78	37.15	12.17	183	38.50	12.28
300	104	38.84	13.79	43	37.91	9.90	147	38.57	12.83
408	107	39.32	11.50	62	37.77	12.21	169	38.75	11.88
73	104	40.19	13.33	55	36.07	11.82	159	38.76	13.84
72	102	38.76	9.99	53	39.15	12.00	155	38.89	10.70
422	102	40.40	10.54	53	37.44	11.34	155	39.39	11.35
193	105	40.38	12.07	61	37.81	10.84	166	39.44	12.06
439	102	39.99	11.88	68	39.21	29.11	170	39.68	20.36
305	100	41.06	10.62	62	38.38	11.52	162	40.03	11.39
60	105	40.52	9.61	59	39.42	12.07	164	40.12	10.58
415	101	40.44	9.87	42	39.92	10.75	143	40.29	10.11
418	103	40.54	11.75	57	40.16	9.70	160	40.40	11.05
49	100	40.87	10.54	39	40.21	9.46	139	40.69	10.25
310	105	42.38	10.60	54	40.09	10.13	159	41.61	10.75
POLLEN PARENTS									
28	570	38.90	10.30	271	38.55	17.93	841	38.79	13.21
448	565	39.08	12.33	353	37.04	12.12	918	38.29	12.52
33	567	39.58	11.51	343	37.39	11.96	910	38.75	11.98
62	575	40.77	11.45	284	38.78	12.63	859	40.12	12.05
TOTAL	2277	39.59	11.57	1251	37.86	13.84	3528	38.97	12.55

TABLE D12. Combined sites analysis of variance for branch length expressed as proportion (%) of tree height (BLT).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	2636.38	1.192	1.356		5.09%		
REP/SITE	4	694.15	1.133	0.682		4.83%		
MALE	3	512.66	0.454	0.374		1.94%		
FEMALE	21	205.33	0.995	0.387	2.561	4.24%	4.659	0.000
S * F	21	34.10	0.090	1.000		0.38%	1.188	0.328
R * F	84	34.72	0.119	0.227		0.51%	1.143	0.217
M * F	63	34.33	0.226	0.197		0.96%	1.410	0.088
S*M*F	63	24.35	0.0	0.290		0.0 %	0.802	0.851
R/S*M*F	242	30.38	2.066	0.430	3.690	8.81%	1.788	0.0
WITHIN	3010	16.99	16.993	0.438	10.585	72.48%		
ADDITIVE GENETIC VARIANCE			3.980	1.550	5.123			
DOMINANCE GENETIC VARIANCE			0.905	0.790	2.443			
TOTAL PHENOTYPIC VARIANCE			21.121		11.801			
PHENOTYPIC VARIANCE HALF-SIB			1.301		2.929			
PHENOTYPIC VARIANCE FULL-SIB			2.436					
HERITABILITY (INDIVIDUAL)			0.188	0.073		%RESPONSE/i =	2.224	
HERITABILITY (HALF-SIB)			0.765	0.298		%RESPONSE/i =	4 480	
HERITABILITY (FULL-SIB)			0.910	0.318				

TABLE D12 (Continued). Analysis of variance for branch length (proportional) on site CLES.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
RLP	2	26046.00	31.069	24.317		1.46%		
MALE	3	40475.55	66.927	45.017		3.14%		
FEMALE	21	14545.11	104.280	42.473	2.580	4.89%	3.871	0.000
R * M	6	1918.16	0.0	5.376		0.0 %	0.702	0.649
R * F	42	3289.56	15.910	22.689		0.75%	1.204	0.216
M * F	63	3200.09	17.738	25.503		0.83%	1.171	0.226
R*M*F	126	2732.59	110.258	40.338	2.653	5.17%	1.530	0.000
WITHIN	2013	1786.35	1786.358	56.279	10.677	83.77%		
ADDITIVE GENETIC VARIANCE			417.121	169.890	5.159			
DOMINANCE GENETIC VARIANCE			70.952	102.011	2.128			
TOTAL PHENOTYPIC VARIANCE			2101.471		11.581			
PHENOTYPIC VARIANCE HALF-SIB			140.414		2.993			
PHENOTYPIC VARIANCE FULL-SIB			294.614					
HERITABILITY (INDIVIDUAL)			0.198	0.081		%RESPONSE/i =	2.299	
HERITABILITY (HALF-SIB)			0.743	0.302		%RESPONSE/i =	4.446	
HERITABILITY (FULL-SIB)			0.641	0.288				

TABLE D12 (Continued). Analysis of variance for branch length (proportional) on site GVWS.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	112203.19	263.289	190.630		10.93%		
MALE	3	19833.77	57.757	40.644		2.40%		
FEMALE	21	9441.28	125.055	52.041	2.960	5.19%	3.258	0.010
R * M	6	3093.35	0.0	15.623		0.0 %	0.918	0.485
R * F	42	3476.84	0.0	47.076		0.0 %	1.032	0.436
M * F	63	2791.21	0.0	47.688		0.0 %	0.828	0.794
R*M*F	116	3370.13	439.609	105.719	5.550	18.25%	2.212	0.0
WITHIN	997	1523.64	1523.649	68.173	10.332	63.24%		
ADDITIVE GENETIC VARIANCE			500.221	208.163	5.920			
DOMINANCE GENETIC VARIANCE			0.0	190.754	0.0			
TOTAL PHENOTYPIC VARIANCE			2146.070		12.263			
PHENOTYPIC VARIANCE HALF-SIB			184.386		3.594			
PHENOTYPIC VARIANCE FULL-SIB			425.958					
HERITABILITY (INDIVIDUAL)			0.233	0.097		%RESPONSE/i =	2.858	
HERITABILITY (HALF-SIB)			0.678	0.282		%RESPONSE/i =	4.876	
HERITABILITY (FULL-SIB)			0.429	0.244				

TABLE D13. Means and coefficients of variation for bole taper (TAPER) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

	CLES			GVWS			COMBINED		
GROUP	N	MEAN m/mm	CV %	N	MEAN m/mm	CV %	N	MEAN m/mm	CV %
SEED PARENTS									
300	104	16.39	25.40	43	16.16	27.58	147	16.32	25.96
315	104	17.31	23.70	51	17.94	24.38	155	17.52	23.92
57	105	18.14	25.84	66	17.90	20.07	171	18.05	23.76
60	105	17.94	24.74	59	18.78	24.27	164	18.25	24.59
49	100	18.10	24.63	39	18.84	23.90	139	18.31	24.40
193	105	17.86	24.17	61	19.32	27.66	166	18.40	25.86
408	107	18.46	24.21	62	18.77	22.98	169	18.57	23.70
499	104	18.58	19.87	65	18.80	22.18	169	18.67	20.74
623	103	18.18	31.14	62	19.51	25.85	165	18.68	29.23
73	104	18.62	25.82	55	19.21	23.39	159	18.82	24.94
310	105	18.64	26.00	54	19.67	28.80	159	18.99	27.09
303	102	19.47	21.92	60	18.24	20.86	162	19.01	21.74
415	101	18.50	24.69	42	20.36	34.32	143	19.04	28.53
549	107	18.54	19.95	61	20.38	26.23	168	19.21	23.13
314	105	19.71	27.09	78	18.64	21.12	183	19.26	24.98
323	105	20.25	27.58	48	18.41	27.11	153	19.67	27.74
110	102	20.15	27.65	52	18.91	19.29	154	19.73	25.48
418	103	19.85	23.81	57	20.86	22.81	160	20.21	23.49
422	102	20.35	28.94	53	20.10	21.49	155	20.27	26.60
439	102	20.16	23.27	68	20.46	27.31	170	20.28	24.93
305	100	20.49	24.32	62	19.96	20.63	162	20.29	23.00
72	102	19.72	22.23	53	22.27	19.45	155	20.59	21.94
POLLEN PARENTS									
448	565	18.20	23.92	353	18.74	26.91	918	18.41	25.18
28	570	18.55	26.94	271	18.81	24.54	841	18.64	26.17
33	567	19.48	27.73	343	19.08	23.51	910	19.33	26.27
62	575	19.27	22.82	284	20.58	23.02	859	19.70	23.11
TOTAL	2277	18.88	25.59	1251	19.27	24.83	3528	19.01	25.33

TABLE D14. Combined sites analysis of variance for bole taper (TAPER).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	124.1270	0.0	0.0781		0.0 %		
REP/SITE	4	81.8177	0.1003	0.0823		0.42%		
MALE	4	321.3152	0.2301	0.2394		0.96%		
FEMALE	3	160.0427	0.5880	0.3114	4.033	2.45%	2.617	0.008
S * F	21	43.9181	0.2897	0.01		1.21%	1.830	0.084
R * F	84	33.8206	0.0308	0.2248		0.13%	1.058	0.365
M * F	63	39.3816	0.4402	0.2115		1.84%	1.778	0.012
S*M*F	63	22.1455	0.0	0.2767		0.0 %	0.693	0.958
R/S*M*F	242	31.9671	1.7969	0.4538	7.050	7.49%	1.573	0.000
WITHIN	3010	20.3199	20.3199	0.5236	23.707	84.72%		
ADDITIVE GENETIC VARIANCE			2.3521	1.2457	8.066			
DOMINANCE GENETIC VARIANCE			1.7606	0.8460	6.978			
TOTAL PHENOTYPIC VARIANCE			23.8857		25.704			
PHENOTYPIC VARIANCE HALF-SIB			1.034		5.348			
PHENOTYPIC VARIANCE FULL-SIB			2.058					
HERITABILITY-(INDIVIDUAL)			0.098	0.052		%RESPONSE/I =	2.531	
HERITABILITY (HALF-SIB)			0.569	0.301		%RESPONSE/I =	6.083	
HERITABILITY (FULL-SIB)			0.785	0.303				

TABLE D14 (Continued). Analysis of variance for trait TAPER on site CLES

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	2403.84	0.749	2.768		0.03%		
MALE	3	20471.30	32.170	22.848		1.36%		
FEMALE	21	12447.85	90.825	36.596	5.049	3.85%	4.074	0.001
R * M	6	2041.76	0.0	5.774		0.0 %	0.653	0.687
R * F	42	2928.76	0.0	21.455		0.0 %	0.937	0.585
M * F	63	3252.12	4.529	26.861		0.19%	1.040	0.418
R*M*F	126	3125.57	118.170	46.191	5.759	5.01%	1.480	0.001
WITHIN	2013	2111.43	2111.434	66.520	24.344	89.55%		
ADDITIVE GENETIC VARIANCE			363.299	146.382	10.098			
DOMINANCE GENETIC VARIANCE			18.116	107.443	2.255			
TOTAL PHENOTYPIC VARIANCE			2357.126		25.722			
PHENOTYPIC VARIANCE HALF-SIB			122.153		5.855			
PHENOTYPIC VARIANCE FULL-SIB			248.379					
HERITABILITY (INDIVIDUAL)			0.154	0.062		%RESPONSE/i =	3.964	
HERITABILITY (HALF-SIB)			0.744	0.300		%RESPONSE/i =	8.707	
HERITABILITY (FULL-SIB)			0.513	0.295				

TABLE D14 (Continued). Analysis of variance for trait TAPER on site GVWS

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	15565.22	32.448	26.598		1.36%		
MALE	3	21970.21	66.708	44.792		2.79%		
FEMALE	21	7579.28	78.867	43.495	4.609	3.30%	2.181	0.041
R * M	6	2003.48	0.0	10.601		0.0 %	0.612	0.720
R * F	42	3771.26	4.132	49.802		0.17%	1.152	0.275
M * F	63	2978.50	0.0	49.023		0.0 %	0.910	0.656
R*M*F	116	3273.99	333.881	103.425	9.484	13.98%	1.749	0.000
WITHIN	997	1871.59	1871.597	83.742	22.454	78.39%		
ADDITIVE GENETIC VARIANCE			315.469	173.979	9.218			
DOMINANCE GENETIC VARIANCE			0.0	196.091	0.0			
TOTAL PHENOTYPIC VARIANCE			2355.185		25.188			
PHENOTYPIC VARIANCE HALF-SIB			137.841		6.094			
PHENOTYPIC VARIANCE FULL-SIB			381.787					
HERITABILITY (INDIVIDUAL)			0.134	0.074		%RESPONSE/I =	3.374	
HERITABILITY (HALF-SIB)			0.572	0.316		%RESPONSE/I =	6.973	
HERITABILITY (FULL-SIB)			0.381	0.228				

TABLE D15. Means and coefficients of variation for sinuosity score (SIN) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

GROUP	CLES N	CLES MEAN cm	CLES CV %	GVWS N	GVWS MEAN cm	GVWS CV %	COMBINED N	COMBINED MEAN cm	COMBINED CV %
SEED PARENTS									
303	104	31.73	253.28	85	43.53	211.05	189	37.04	231.39
305	100	34.00	222.07	89	53.93	207.41	189	43.39	218.16
415	101	27.72	239.92	87	64.37	201.00	188	44.68	228.23
193	106	66.98	179.30	87	28.74	230.76	193	49.74	203.25
314	105	58.10	183.01	89	41.57	207.71	194	50.52	193.55
439	102	56.86	192.50	90	50.00	203.89	192	53.65	197.19
57	106	44.34	256.83	91	68.13	160.60	197	55.33	202.76
300	105	31.43	222.00	83	93.98	162.27	188	59.04	199.50
422	103	59.22	159.38	94	78.72	171.61	197	68.53	168.87
49	100	38.00	200.66	84	105.95	184.95	184	69.02	213.49
110	102	64.71	163.68	83	87.95	199.63	185	75.14	188.37
499	105	52.38	183.60	90	103.33	144.67	195	75.90	165.93
315	104	57.69	186.61	83	101.20	167.98	187	77.01	181.94
72	102	65.69	161.02	77	100.00	169.36	179	80.45	170.82
418	104	73.08	150.42	87	91.95	172.52	191	81.68	164.41
310	105	90.48	164.03	78	92.31	150.97	183	91.26	158.05
73	104	99.04	150.55	89	105.62	124.73	193	102.07	138.17
60	105	113.33	147.88	93	94.62	200.37	198	104.55	170.32
623	103	114.56	127.26	91	164.84	155.16	194	138.14	149.01
408	107	107.48	147.78	90	177.78	107.58	197	139.59	127.11
549	107	138.32	114.37	88	175.00	132.04	195	154.87	125.79
323	105	161.90	106.08	88	203.41	114.62	193	180.83	112.03
POLLEN PARENTS									
33	568	47.89	214.05	485	71.34	192.33	1053	58.69	204.90
28	571	58.32	185.46	460	70.87	199.44	1031	63.92	194.24
62	578	69.38	156.80	487	107.19	153.43	1065	86.67	159.58
448	568	114.44	140.61	484	136.57	150.27	1052	124.62	146.75
TOTAL	2285	72.47	172.26	1916	96.82	172.17	4201	83.58	174.59

TABLE D16. Combined sites analysis of variance for stem sinuosity (SIN).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	617589.50	241.833	243.728		1.10%		
REP/SITE	4	99167.38	119.498	82.447		0.55%		
MALE	3	940150.00	871.317	566.485		3.98%		
FEMALE	21	293517.63	1340.730	460.583	43.812	6.12%	7.804	0.000
S * F	21	38925.22	0.0	1.000		0.0 %	0.946	0.541
R * F	84	36391.14	181.016	194.650		0.83%	1.203	0.140
M * F	63	33691.33	0.0	187.552		0.0 %	0.962	0.560
S*M*F	63	35005.11	191.760	285.694		0.88%	1.157	0.218
R/S*M*F	252	30259.53	1660.239	347.203	48.754	7.58%	1.753	0.0
WITHIN	3673	17261.99	17261.992	402.696	157.206	78.85%		
ADDITIVE GENETIC VARIANCE			5362.918	1842.330	87.624			
DOMINANCE GENETIC VARIANCE			0.0	750.208	0.0			
TOTAL PHENOTYPIC VARIANCE			21530.723		175.571			
PHENOTYPIC VARIANCE HALF-SIB			1552.822		47.150			
PHENOTYPIC VARIANCE FULL-SIB			2940.741					
HERITABILITY (INDIVIDUAL)			0.249	0.086		%RESPONSE/i =	43.732	
HERITABILITY (HALF-SIB)			0.863	0.297		%RESPONSE/i =	81.421	
HERITABILITY (FULL-SIB)			0.912	0.313				

TABLE D16 (Continued). Combined sites analysis of variance for stem sinuosity (transformed).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	426.82	0.164	0.169		0.83%		
REP/SITE	4	74.64	0.082	0.062		0.42%		
MALE	3	885.60	0.823	0.534		4.18%		
FEMALE	21	275.72	1.268	0.432	8.783	6.43%	8.194	0.000
S * F	21	35.90	0.0	1.000		0.0 %	0.936	0.552
R * F	84	31.72	0.183	0.169		0.93%	1.239	0.106
M * F	63	30.01	0.0	0.169		0.0 %	0.930	0.612
S*M*F	63	32.26	0.275	0.260		1.40%	1.260	0.111
R/S*M*F	252	25.61	1.275	0.294	8.807	6.47%	1.639	0.0
WITHIN	3673	15.63	15.629	0.365	30.832	79.29%		
ADDITIVE GENETIC VARIANCE			5.073	1.729	17.566			
DOMINANCE GENETIC VARIANCE			0.0	0.676	0.0			
TOTAL PHENOTYPIC VARIANCE			19.465		34.409			
PHENOTYPIC VARIANCE HALF-SIB			1.467		9.445			
PHENOTYPIC VARIANCE FULL-SIB			2.764					
HERITABILITY (INDIVIDUAL)			0.261	0.089		%RESPONSE/i =	8.968	
HERITABILITY (HALF-SIB)			0.865	0.295		%RESPONSE/i =	16.335	
HERITABILITY (FULL-SIB)			0.918	0.313				

TABLE D17. Means and coefficients of variation for forking occurence (FORK) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

GROUP	CLES N	MEAN cm	CV %	GVWS N	MEAN cm	CV %	COMBINED N	MEAN cm	CV %
SEED PARENTS									
549	107	11.22	308.08	88	9.09	359.12	195	10.26	327.95
314	105	19.10	251.63	89	10.11	334.85	194	14.43	281.94
72	102	15.69	280.04	77	16.88	278.52	179	16.20	278.75
439	102	21.57	240.85	90	20.00	239.38	192	20.83	239.79
323	105	18.10	239.68	88	25.00	203.42	193	21.24	220.92
415	101	15.84	292.46	87	27.59	189.01	188	21.28	231.81
110	102	19.61	215.77	83	25.30	212.42	185	22.16	215.35
60	105	22.86	212.41	93	21.51	236.01	198	22.22	222.64
73	104	25.00	191.06	89	20.22	237.83	193	22.80	209.91
499	105	19.05	242.51	90	28.89	195.84	195	23.59	217.67
408	107	19.63	215.03	90	28.89	209.14	197	23.86	215.45
57	106	26.42	204.38	91	24.18	241.51	197	25.38	220.36
303	104	31.73	177.11	85	18.82	238.91	189	25.93	199.51
422	103	18.45	224.51	94	35.11	175.78	197	26.40	199.36
310	105	25.71	179.09	78	34.62	185.22	183	29.51	184.71
193	106	34.91	163.23	87	22.99	206.62	193	29.53	179.84
418	104	28.85	165.04	87	32.18	198.19	191	30.37	182.55
305	100	31.00	175.76	89	35.96	183.95	189	33.33	180.43
300	105	38.10	176.02	83	32.53	186.61	188	35.64	180.20
315	104	32.69	172.84	83	42.17	161.94	187	36.90	168.08
623	103	48.54	152.27	91	38.46	188.96	194	43.81	167.35
49	100	43.00	145.04	84	47.62	132.32	184	45.11	138.63
POLLEN PARENTS									
448	568	18.84	234.71	484	15.70	252.73	1052	17.40	242.59
62	578	18.51	232.83	487	22.18	245.49	1065	20.19	240.88
33	568	26.94	199.53	485	34.64	181.74	1053	30.48	191.13
28	571	38.53	159.49	460	36.52	170.82	1031	37.63	164.34
TOTAL	2285	25.69	201.53	1916	27.14	207.08	4201	26.35	204.30

TABLE D18. Combined sites analysis of variance for forking incidence (FORK).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	2192.92	0.0	10.795		0.0 %		
REP/SITE	4	37622.65	44.352	31.367		1.47%		
MALE	3	91494.50	80.512	55.351		2.66%		
FEMALE	21	14070.04	57.460	23.182	28.768	1.90%	4.501	0.012
S * F	21	3226.61	7.569	1.000		0.25%	1.259	0.341
R * F	84	3261.43	0.0	20.811		0.0 %	0.672	0.983
M * F	63	4053.76	0.0	23.214		0.0 %	0.976	0.539
S*M*F	63	4154.51	0.0	36.108		0.0 %	0.856	0.766
R/S*M*F	252	4853.72	298.362	55.586	65.553	9.86%	1.928	0.0
WITHIN	3673	2517.93	2517.934	58.739	190.433	83.23%		
ADDITIVE GENETIC VARIANCE			229.841	92.728	57.535			
DOMINANCE GENETIC VARIANCE			0.0	92.857	0.0			
TOTAL PHENOTYPIC VARIANCE			2980.768		207.197			
PHENOTYPIC VARIANCE HALF-SIB			86.620		35.321			
PHENOTYPIC VARIANCE FULL-SIB			239.694					
HERITABILITY (INDIVIDUAL)			0.077	0.031		%RESPONSE/i =	15.977	
HERITABILITY (HALF-SIB)			0.663	0.268		%RESPONSE/f =	46.861	
HERITABILITY (FULL-SIB)			0.479	0.193				

TABLE D18 (continued). Combined sites analysis of variance for forking incidence (transformed).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	1.83	0.0	0.016		0.0 %		
REP/SITE	4	56.50	0.067	0.047		1.49%		
MALE	4	139.06	0.123	0.084		2.73%		
FEMALE	3	21.36	0.087	0.035	2.665	1.93%	4.404	0.010
S * F	21	4.84	0.013	1.000		0.30%	1.326	0.313
R * F	84	4.86	0.0	0.031		0.0 %	0.670	0.984
M * F	63	6.05	0.0	0.034		0.0 %	1.002	0.497
S*M*F	63	6.04	0.0	0.053		0.0 %	0.833	0.805
R/S*M*F	252	7.25	0.449	0.083	6.064	9.97%	1.944	0.0
WITHIN	3673	3.73	3.734	0.087	17.492	82.98%		
ADDITIVE GENETIC VARIANCE			0.347	0.140	5.331			
DOMINANCE GENETIC VARIANCE			0.0	0.137	0.0			
TOTAL PHENOTYPIC VARIANCE			4.433		19.059			
PHENOTYPIC VARIANCE HALF-SIB			0.131		3.279			
PHENOTYPIC VARIANCE FULL-SIB			0.362					
HERITABILITY (INDIVIDUAL)			0.078	0.032		%RESPONSE/i =	1.491	
HERITABILITY (HALF-SIB)			0.661	0.268		%RESPONSE/i =	4.333	
HERITABILITY (FULL-SIB)			0.480	0.194				

TABLE D19. Means and coefficients of variation for lammas flush incidence (LAFL) at the Cowichan Lake (CLES) and Victoria Watershed (GVWS) sites and combined over sites.

GROUP	CLES N	CLES MEAN cm	CLES CV %	GVWS N	GVWS MEAN cm	GVWS CV %	COMBINED N	COMBINED MEAN cm	COMBINED CV %
SEED PARENTS									
72	102	1.96	710.59	77	2.60	616.39	179	2.23	663.30
314	105	1.90	721.06	89	3.37	538.44	194	2.58	616.41
315	104	2.88	583.04	83	7.23	360.41	187	4.81	445.92
415	101	4.95	440.36	87	6.90	484.10	188	5.85	473.55
549	107	6.54	379.74	88	5.68	409.77	195	6.15	391.52
323	105	3.81	622.45	88	9.09	359.12	193	6.22	453.33
499	105	4.76	449.36	90	8.89	400.67	195	6.67	432.56
305	100	12.00	296.82	89	5.62	491.85	189	8.99	357.79
439	102	10.78	317.13	90	10.00	425.32	192	10.42	367.02
57	106	9.43	401.40	91	13.19	323.89	197	11.17	359.23
300	105	11.43	304.91	83	10.84	381.39	188	11.17	337.99
422	103	16.50	282.62	94	6.38	385.02	197	11.68	325.55
408	107	14.02	316.73	90	8.89	400.67	197	11.68	347.79
310	105	9.52	309.70	78	17.95	280.28	183	13.11	303.59
193	106	18.87	243.85	87	8.05	340.02	193	13.99	278.87
110	102	12.75	285.18	83	16.87	274.96	185	14.59	281.51
303	104	13.46	311.54	85	17.65	340.63	189	15.34	331.19
418	104	17.31	247.40	87	14.94	280.03	191	16.23	260.51
73	104	22.12	251.69	89	15.73	316.39	193	19.17	276.39
623	103	34.95	186.67	91	20.88	272.03	194	28.35	217.54
60	105	28.57	246.12	93	34.41	212.07	198	31.31	228.20
49	100	41.00	170.17	84	21.43	251.69	184	32.07	198.42
POLLEN									
448	568	5.28	438.51	484	3.51	585.15	1052	4.47	492.58
62	578	7.61	381.44	487	4.11	575.83	1065	6.01	445.19
33	568	19.72	275.98	485	18.97	267.42	1053	19.37	272.17
28	571	21.72	232.31	460	22.61	254.94	1031	22.11	243.06
TOTAL	2285	13.57	309.98	1916	12.16	345.81	4201	12.93	325.36

TABLE D20. Combined sites analysis of variance for lammas flushing incidence (LAFL).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	2060.12	0.0	2.960		0.0 %		
REP/SITE	4	9491.52	6.902	8.372		0.37%		
MALE	4	85578.50	78.666	51.583		4.26%		
FEMALE	3	13681.92	48.136	21.913	53.679	2.61%	3.054	0.002
S * F	21	2371.12	12.409	1.000		0.67%	1.944	0.118
R * F	84	1722.73	0.0	10.800		0.0 %	0.703	0.970
M * F	63	4054.63	44.042	17.175		2.39%	2.083	0.002
S*M*F	63	1946.30	0.0	17.288		0.0 %	0.795	0.861
R/S*M*F	252	2449.21	118.561	28.160	84.244	6.42%	1.610	0.0
WITHIN	3673	1521.03	1521.027	35.483	301.743	82.37%		
ADDITIVE GENETIC VARIANCE			192.543	87.652	107.358			
DOMINANCE GENETIC VARIANCE			176.169	68.701	102.691			
TOTAL PHENOTYPIC VARIANCE			1839.612		331.843			
PHENOTYPIC VARIANCE HALF-SIB			78.110		68.379			
PHENOTYPIC VARIANCE FULL-SIB			222.180					
HERITABILITY (INDIVIDUAL)			0.105	0.048		%RESPONSE/i =	34.732	
HERITABILITY (HALF-SIB)			0.616	0.281		%RESPONSE/i =	84.278	
HERITABILITY (FULL-SIB)			0.632	0.197				

TABLE D20 (continued). Combined sites analysis of variance for lammas flushing incidence (transformed).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	4.15	0.0	0.005		0.0 %		
REP/SITE	4	14.35	0.010	0.013		0.38%		
MALE	3	125.83	0.116	0.076		4.36%		
FEMALE	21	19.66	0.068	0.032	2.487	2.58%	2.983	0.002
S * F	21	3.51	0.019	1.000		0.71%	1.961	0.115
R * F	84	2.47	0.0	0.015		0.0 %	0.704	0.970
M * F	63	5.91	0.064	0.025		2.43%	2.088	0.002
S*M*F	63	2.83	0.0	0.025		0.0 %	0.806	0.845
R/S*M*F	252	3.51	0.171	0.040	3.936	6.45%	1.610	0.0
WITHIN	3673	2.18	2.176	0.051	14.038	82.06%		
ADDITIVE GENETIC VARIANCE			0.273	0.126	4.975			
DOMINANCE GENETIC VARIANCE			0.258	0.100	4.831			
TOTAL PHENOTYPIC VARIANCE			2.641		15.468			
PHENOTYPIC VARIANCE HALF-SIB			0.112		3.186			
PHENOTYPIC VARIANCE FULL-SIB			0.322					
HERITABILITY (INDIVIDUAL)			0.103	0.048		%RESPONSE/i =	1.600	
HERITABILITY (HALF-SIB)			0.610	0.281		%RESPONSE/i =	3.884	
HERITABILITY (FULL-SIB)			0.624	0.196				

TABLE D21. Components of variance and covariance for traits DM12 and BN.

FOR VARIABLES	DM12			BN			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	4.8518	S.E.	2.1706	637.1118	S.E.	232.4150	37.2200
ADDITIVE GENETIC VARIANCE	19.4072	S.E.	8.6824	2548.4473	S.E.	929.6599	148.8795
DOMINANCE GENETIC VARIANCE	6.1308	S.E.	8.4330	0.0	S.E.	631.8674	-3.0654
PHENOTYPIC VARIANCE INDIVIDUAL	138.3089			13522.1914			466.0059
PHENOTYPIC VARIANCE HALF-SIB	7.9453			776.3027			60.5851
PHENOTYPIC VARIANCE FULL-SIB	14.8172			1312.1626			124.8149
HERITABILTY FOR INDIVIDUAL SELECTION	0.1403	S.E.	0.0628	0.1885	S.E.	0.0688	0.1626
COEFFICIENT OF VARIATION (PI)	14.4858			21.7566			
%RESPONSE /I (INDIVIDUAL)	2.0326			4.1003			
HERITABILTY FOR HALF-SIB SELECTION	0.6106	S.E.	1.0928	0.8207	S.E.	1.1975	0.7079
COEFFICIENT OF VARIATION (PHS)	3.4719			5.2129			
%RESPONSE /I (HALF-SIB)	4.2403	CRy=	3.2908	8.5565	CRx=	4.9410	
GENETIC CORRELATIONS	0.6694	S.E.	0.1576				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0.3408						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	0.7714						
ENVIRONMENTAL CORRELATIONS	0.2776						

TABLE D22. Components of variance and covariance for traits DM12 and BA.

FOR VARIABLES	DM12			BA			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	4.8518	S.E.	2.1706	8.8509	S.E.	2.8756	1.1636
ADDITIVE GENETIC VARIANCE	19.4072	S.E.	8.6824	35.4036	S.E.	11.5024	4.6544
DOMINANCE GENETIC VARIANCE	6.1308	S.E.	8.4330	3.9828	S.E.	2.0089	-5.0568
PHENOTYPIC VARIANCE INDIVIDUAL	138.3089			48.6369			-2.8303
PHENOTYPIC VARIANCE HALF-SIB	7.9453			9.6585			0.6388
PHENOTYPIC VARIANCE FULL-SIB	14.8172			12.4912			-0.1134
HERITABILTY FOR INDIVIDUAL SELECTION	0.1403	S.E.	0.0628	0.7279	S.E.	0.2365	0.3196
COEFFICIENT OF VARIATION (PI)	14.4858			10.6078			
%RESPONSE /i (INDIVIDUAL)	2.0326			7.7216			
HERITABILTY FOR HALF-SIB SELECTION	0.6106	S.E.	1.0928	0.9164	S.E.	1.1909	0.7481
COEFFICIENT OF VARIATION (PHS)	3.4719			4.7271			
%RESPONSE /i (HALF-SIB)	4.2403	CRy=	0.9224	8.6638	CRx=	1.2558	
GENETIC CORRELATIONS	0.1776	S.E.	0.2611				
PHENOTYPIC CORRELATIONS INDIVIDUAL	-0.0345						
PHENOTYPIC CORRELATIONS H.S FAMILIES	0.0729						
ENVIRONMENTAL CORRELATIONS	-0.1887						

TABLE D23. Components of variance and covariance for traits DM12 and BT.

FOR VARIABLES	DM12			BT			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	4.8518	S.E.	2.1706	13.0385	S.E.	8.7298	1.6984
ADDITIVE GENETIC VARIANCE	19.4072	S.E.	8.6824	52.1540	S.E.	34.9191	6.7934
DOMINANCE GENETIC VARIANCE	6.1308	S.E.	8.4330	56.1908	S.E.	50.6246	13.5694
PHENOTYPIC VARIANCE INDIVIDUAL	138.3089			997.6316			290.2927
PHENOTYPIC VARIANCE HALF-SIB	7.9453			29.7812			7.7853
PHENOTYPIC VARIANCE FULL-SIB	14.8172			96.6582			21.6033
HERITABILTY FOR INDIVIDUAL SELECTION	0.1403	S.E.	0.0628	0.0523	S.E.	0.0350	0.0856
COEFFICIENT OF VARIATION (PI)	14.4858			16.2497			
%RESPONSE /I (INDIVIDUAL)	2.0326			0.8495			
HERITABILTY FOR HALF-SIB SELECTION	0.6106	S.E.	1.0928	0.4378	S.E.	1.1725	0.5171
COEFFICIENT OF VARIATION (PHS)	3.4719			2.8076			
%RESPONSE /I (HALF-SIB)	4.2403	CRy=	0.7667	2.4584	CRx=	0.6200	
GENETIC CORRELATIONS	0.2135	S.E.	0.3694				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0.7815						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	0.5061						
ENVIRONMENTAL CORRELATIONS	0.6455						

TABLE D24. Components of variance and covariance for traits DM12 and BTT.

FOR VARIABLES	DM12			BTT			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	4.8518	S.E.	2.1706	65.8913	S.E.	26.1388	-14.6066
ADDITIVE GENETIC VARIANCE	19.4072	S.E.	8.6824	263.5652	S.E.	104.5552	-58.4265
DOMINANCE GENETIC VARIANCE	6.1308	S.E.	8.4330	32.8068	S.E.	51.3189	-3.1042
PHENOTYPIC VARIANCE INDIVIDUAL	138.3089			1008.7383			-36.4907
PHENOTYPIC VARIANCE HALF-SIB	7.9453			84.1252			-16.2475
PHENOTYPIC VARIANCE FULL-SIB	14.8172			169.3226			-21.2929
HERITABILTY FOR INDIVIDUAL SELECTION	0.1403	S.E.	0.0628	0.2613	S.E.	0.1036	0.1915
COEFFICIENT OF VARIATION (PI)	14.4858			11.6439			
%RESPONSE /I (INDIVIDUAL)	2.0326			3.0423			
HERITABILTY FOR HALF-SIB SELECTION	0.6106	S.E.	1.0928	0.7833	S.E.	1.2429	0.6916
COEFFICIENT OF VARIATION (PHS)	3.4719			3.3626			
%RESPONSE /I (HALF-SIB)	4.2403	CRy=	-3.9231	5.2675	CRx=	-3.7996	
GENETIC CORRELATIONS	-0.8169	S.E.	0.0991				
PHENOTYPIC CORRELATIONS INDIVIDUAL	-0.0977						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	-0.6284						
ENVIRONMENTAL CORRELATIONS	0.0737						

TABLE D25. Components of variance and covariance for traits BN and BA.

FOR VARIABLES	BN			BA			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	637.1118	S.E.	232.4150	8.8509	S.E.	2.8756	14.3451
ADDITIVE GENETIC VARIANCE	2548.4473	S.E.	929.6599	35.4036	S.E.	11.5024	57.3802
DOMINANCE GENETIC VARIANCE	0.0	S.E.	631.8674	3.9828	S.E.	2.0089	-1.9914
PHENOTYPIC VARIANCE INDIVIDUAL	13522.1914			48.6369			226.3008
PHENOTYPIC VARIANCE HALF-SIB	776.3027			9.6585			32.3118
PHENOTYPIC VARIANCE FULL-SIB	1312.1626			12.4912			99.2004
HERITABILTY FOR INDIVIDUAL SELECTION	0.1885	S.E.	0.0688	0.7279	S.E.	0.2365	0.3704
COEFFICIENT OF VARIATION (PI)	21.7566			10.6078			
%RESPONSE /I (INDIVIDUAL)	4.1003			7.7216			
HERITABILTY FOR HALF-SIB SELECTION	0.8207	S.E.	1.1975	0.9164	S.E.	1.1909	0.8672
COEFFICIENT OF VARIATION (PHS)	5.2129			4.7271			
%RESPONSE /I (HALF-SIB)	8.5565	CRy=	1.7272	8.6638	CRx=	1.5662	
GENETIC CORRELATIONS	0.1910	S.E.	0.2345				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0.2790						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	0.3732						
ENVIRONMENTAL CORRELATIONS	0.4433						

TABLE D26. Components of variance and covariance for traits BN and BTT.

FOR VARIABLES	BN			BTT			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	637.1118	S.E.	232.4150	65.8913	S.E.	26.1388	-120.5745
ADDITIVE GENETIC VARIANCE	2548.4473	S.E.	929.6599	263.5652	S.E.	104.5552	-482.2981
DOMINANCE GENETIC VARIANCE	0.0	S.E.	631.8674	32.8068	S.E.	51.3189	-16.4034
PHENOTYPIC VARIANCE INDIVIDUAL	13522.1914			1008.7383			-587.4219
PHENOTYPIC VARIANCE HALF-SIB	776.3027			84.1252			-118.7056
PHENOTYPIC VARIANCE FULL-SIB	1312.1626			169.3226			-199.9982
HERITABILTY FOR INDIVIDUAL SELECTION	0.1885	S.E.	0.0688	0.2613	S.E.	0.1036	0.2219
COEFFICIENT OF VARIATION (PI)	21.7566			11.6439			
%RESPONSE /i (INDIVIDUAL)	4.1003			3.0423			
HERITABILTY FOR HALF-SIB SELECTION	0.8207	S.E.	1.1975	0.7833	S.E.	1.2429	0.8018
COEFFICIENT OF VARIATION (PHS)	5.2129			3.3626			
%RESPONSE /i (HALF-SIB)	8.5565	CRy=	-4.9192	5.2675	CRx=	-3.1731	
GENETIC CORRELATIONS	-0.5885	S.E.	0.1158				
PHENOTYPIC CORRELATIONS INDIVIDUAL	-0.1591						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	-0.4645						
ENVIRONMENTAL CORRELATIONS	-0.0368						

TABLE D27. Means and standard deviations for knottiness index (KI) over both sites.

GROUP	COUNT	MEAN	STANDARD DEVIATION	STANDARD ERROR	MINIMUM	MAXIMUM	95 PCT CONF INT FOR MEAN		
SEED PARENTS									
300	147	25.8267	7.4739	.6164	10.7311	47.1342	24.6085	TO	27.0450
193	166	28.7409	8.1277	.6308	13.0243	57.0507	27.4954	TO	29.9865
315	155	28.8089	9.7207	.7808	10.2643	67.4298	27.2664	TO	30.3513
49	139	29.7855	9.2425	.7839	15.4108	57.6035	28.2354	TO	31.3355
314	183	30.1711	9.9930	.7387	12.6259	74.9487	28.7135	TO	31.6286
73	159	30.5226	9.2288	.7319	15.1229	89.8677	29.0771	TO	31.9682
310	159	30.5444	11.0273	.8745	10.4307	83.6777	28.8172	TO	32.2717
60	164	30.6695	10.6735	.8335	4.9164	62.8962	29.0238	TO	32.3153
72	155	30.7905	9.7992	.7871	5.4127	53.6272	29.2356	TO	32.3454
415	143	31.0496	9.3946	.7856	12.4129	62.0864	29.4966	TO	32.6026
439	170	31.2549	10.3964	.7974	9.1114	71.2551	29.6808	TO	32.8290
110	154	31.3072	9.4954	.7652	16.2091	63.6287	29.7955	TO	32.8188
499	169	31.3094	9.5930	.7379	11.9886	60.0460	29.8526	TO	32.7662
418	160	31.5488	9.2661	.7325	13.5790	59.2187	30.1020	TO	32.9956
408	169	31.9660	8.4776	.6521	14.9646	55.5237	30.6786	TO	33.2534
549	168	32.1633	8.7404	.6743	10.9531	54.7517	30.8320	TO	33.4947
57	171	32.4989	10.7578	.8227	10.8522	73.3332	30.8750	TO	34.1229
323	153	33.3764	11.3164	.9149	4.4183	66.2064	31.5689	TO	35.1840
623	165	33.9339	9.9908	.7778	12.6121	66.2065	32.3981	TO	35.4697
305	162	33.9977	11.6097	.9121	11.9714	78.4851	32.1964	TO	35.7990
422	155	34.8449	10.4914	.8427	8.1963	62.1096	33.1802	TO	36.5096
303	162	35.3462	11.2436	.8834	13.4678	95.3615	33.6017	TO	37.0907
POLLEN PARENTS									
62	859	29.8380	9.2682	.3162	10.9531	66.4334	29.2173	TO	30.4587
24	841	31.1511	10.4379	.3599	5.4127	89.8677	30.4446	TO	31.8575
33	910	31.9319	9.8152	.3254	4.4183	74.9487	31.2934	TO	32.5705
448	918	32.6107	10.5160	.3471	4.9164	95.3615	31.9295	TO	33.2918
TOTAL	3528	31.4126	10.0741	.1696	4.4183	95.3615	31.0800	TO	31.7451

TABLE D28. Combined sites analysis of variance for knottiness index (KI) x10.

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
SITE	1	9688850.00	5865.523	4899.680		43.60%		
REP/SITE	4	233768.44	366.884	229.948		2.73%		
MALE	4	75104.75	72.819	54.867		0.54%		
FEMALE	3	66856.06	279.607	129.687	4.294	2.08%	3.272	0.006
S * F	-21	19256.72	96.840	1.000		0.72%	1.542	0.119
R * F	84	12663.69	82.299	81.140		0.61%	1.251	0.097
M * F	63	11126.70	11.498	69.510		0.09%	1.118	0.329
S*M*F	63	9949.73	0.0	112.296		0.0 %	0.983	0.519
R/S*M*F	242	10122.07	635.125	143.385	6.471	4.72%	1.686	0.0
WITHIN	3010	6005.36	6005.363	154.749	19.899	44.64%		
ADDITIVE GENETIC VARIANCE			1118.428	518.749	8.587			
DOMINANCE GENETIC VARIANCE			45.991	278.041	1.741			
TOTAL PHENOTYPIC VARIANCE			7219.480		21.818			
PHENOTYPIC VARIANCE HALF-SIB			403.222		5.156			
PHENOTYPIC VARIANCE FULL-SIB			617.163					
HERITABILITY (INDIVIDUAL)			0.155	0.072		%RESPONSE/I =	3.380	
HERITABLITY (HALF-SIB)			0.693	0.322		%RESPONSE/I =	7.151	
HERITABILITY (FULL-SIB)			0.925	0.420				

TABLE D29. Components of variance and covariance for traits KI and BT.

FOR VARIABLES	KI			BT			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	279.6069	S.E.	129.6874	13.0385	S.E.	8.7298	33.7012
ADDITIVE GENETIC VARIANCE	1118.4277	S.E.	518.7493	52.1540	S.E.	34.9191	134.8044
DOMINANCE GENETIC VARIANCE	45.9912	S.E.	278.0405	56.1908	S.E.	50.6246	-1.6992
PHENOTYPIC VARIANCE INDIVIDUAL	7219.4805			997.6316			1006.9375
PHENOTYPIC VARIANCE HALF-SIB	403.2217			29.7812			40.0529
PHENOTYPIC VARIANCE FULL-SIB	617.1631			96.6582			103.1550
HERITABILTY FOR INDIVIDUAL SELECTION	0.1549	S.E.	0.0719	0.0523	S.E.	0.0350	0.0900
COEFFICIENT OF VARIATION (PI)	21.8176			16.2497			
%RESPONSE /i (INDIVIDUAL)	3.3799			0.8495			
HERITABILTY FOR HALF-SIB SELECTION	0.6934	S.E.	1.2865	0.4378	S.E.	1.1725	0.5510
COEFFICIENT OF VARIATION (PHS)	5.1562			2.8076			
%RESPONSE /i (HALF-SIB)	7.1509	GRy=	3.1714	2.4584	CRx=	1.7269	
GENETIC CORRELATIONS	0.5582	S.E.	0.2713				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0.3752						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	0.3655						
ENVIRONMENTAL CORRELATIONS	0.3631						

TABLE D30. Components of variance and covariance for traits KI and BN.

FOR VARIABLES	KI			BN			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	279.6069	S.E.	129.6874	637.1118	S.E.	232.4150	150.4556
ADDITIVE GENETIC VARIANCE	1118.4277	S.E.	518.7493	2548.4473	S.E.	929.6599	601.8223
DOMINANCE GENETIC VARIANCE	45.9912	S.E.	278.0405	0.0	S.E.	631.8674	-22.9956
PHENOTYPIC VARIANCE INDIVIDUAL	7219.4805			13522.1914			6540.2500
PHENOTYPIC VARIANCE HALF-SIB	403.2217			776.3027			256.9263
PHENOTYPIC VARIANCE FULL-SIB	617.1631			1312.1626			399.2683
HERITABILTY FOR INDIVIDUAL SELECTION	0.1549	S.E.	0.0719	0.1885	S.E.	0.0688	0.1709
COEFFICIENT OF VARIATION (PI)	21.8176			21.7566			
%RESPONSE /i (INDIVIDUAL)	3.3799			4.1003			
HERITABILTY FOR HALF-SIB SELECTION	0.6934	S.E.	1.2865	0.8207	S.E.	1.1975	0.7544
COEFFICIENT OF VARIATION (PHS)	5.1562			5.2129			
%RESPONSE /i (HALF-SIB)	7.1508	CRy=	2.7732	8.5565	CRx=	2.8037	
GENETIC CORRELATIONS	0.3565	S.E.	0.2539				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0.6619						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	0.4592						
ENVIRONMENTAL CORRELATIONS	0.7258						

TABLE D31. Components of variance and covariance for traits KI and BTT.

FOR VARIABLES	KI			BTT			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	279.6069	S.E.	129.6874	65.8913	S.E.	26.1388	71.1642
ADDITIVE GENETIC VARIANCE	1118.4277	S.E.	518.7493	263.5652	S.E.	104.5552	284.6563
DOMINANCE GENETIC VARIANCE	45.9912	S.E.	278.0405	32.8068	S.E.	51.3189	187.9109
PHENOTYPIC VARIANCE INDIVIDUAL	7219.4805			1008.7383			1328.5469
PHENOTYPIC VARIANCE HALF-SIB	403.2217			84.1252			109.4626
PHENOTYPIC VARIANCE FULL-SIB	617.1631			169.3226			224.0980
HERITABILTY FOR INDIVIDUAL SELECTION	0.1549	S.E.	0.0719	0.2613	S.E.	0.1036	0.2012
COEFFICIENT OF VARIATION (PI)	21.8176			11.6439			
%RESPONSE /I (INDIVIDUAL)	3.3799			3.0423			
HERITABILTY FOR HALF-SIB SELECTION	0.6934	S.E.	1.2865	0.7833	S.E.	1.2429	0.7370
COEFFICIENT OF VARIATION (PHS)	5.1562			3.3626			
%RESPONSE /I (HALF-SIB)	7.1509	CRy=	3.9846	5.2675	CRx=	2.5985	
GENETIC CORRELATIONS	0.5243	S.E.	0.2199				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0.4923						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	0.5943						
ENVIRONMENTAL CORRELATIONS	0.4896						

TABLE D32. Components of variance and covariance for traits KI and BT.

FOR VARIABLES	KI			BA			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	279.6069	S.E.	129.6874	8.8509	S.E.	2.8756	-4.9833
ADDITIVE GENETIC VARIANCE	1118.4277	S.E.	518.7493	35.4036	S.E.	11.5024	-19.7335
DOMINANCE GENETIC VARIANCE	45.9912	S.E.	278.0405	3.9828	S.E.	2.0089	-5.4362
PHENOTYPIC VARIANCE INDIVIDUAL	7219.4805			48.6369			-31.1211
PHENOTYPIC VARIANCE HALF-SIB	403.2217			9.6585			-6.0128
PHENOTYPIC VARIANCE FULL-SIB	617.1631			12.4912			-17.2538
HERITABILTY FOR INDIVIDUAL SELECTION	0.1549	S.E.	0.0719	0.7279	S.E.	0.2365	0.3358
COEFFICIENT OF VARIATION (PI)	21.8176			10.6078			
%RESPONSE /I (INDIVIDUAL)	3.3799			7.7216			
HERITABILTY FOR HALF-SIB SELECTION	0.6934	S.E.	1.2865	0.9164	S.E.	1.1909	0.7972
COEFFICIENT OF VARIATION (PHS)	5.1562			4.7271			
%RESPONSE /I (HALF-SIB)	7.1509	CRy=	-0.8152	8.6638	CRx=	-0.7474	
GENETIC CORRELATIONS	-0.0992	S.E.	0.2718				
PHENOTYPIC CORRELATIONS INDIVIDUAL	-0.0525						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	-0.0963						
ENVIRONMENTAL CORRELATIONS	-0.0401						

TABLE D33. Components of variance and covariance for traits KI and DM12.

FOR VARIABLES	KI			DM12			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	279.6069	S.E.	129.6874	4.8518	S.E.	2.1706	-11.8416
ADDITIVE GENETIC VARIANCE	1118.4277	S.E.	518.7493	19.4072	S.E.	8.6824	-47.3666
DOMINANCE GENETIC VARIANCE	45.9912	S.E.	278.0405	6.1308	S.E.	8.4330	-26.0610
PHENOTYPIC VARIANCE INDIVIDUAL	7219.4805			138.3089			9.5723
PHENOTYPIC VARIANCE HALF-SIB	403.2217			7.9453			-16.8413
PHENOTYPIC VARIANCE FULL-SIB	617.1631			14.8172			-19.4048
HERITABILTY FOR INDIVIDUAL SELECTION	0.1549	S.E.	0.0719	0.1403	S.E.	0.0628	0.1474
COEFFICIENT OF VARIATION (PI)	21.8176			14.4858			
%RESPONSE /I (INDIVIDUAL)	3.3799			2.0326			
HERITABILTY FOR HALF-SIB SELECTION	0.6934	S.E.	1.2865	0.6106	S.E.	1.0928	0.6507
COEFFICIENT OF VARIATION (PHS)	5.1562			3.4719			
%RESPONSE /I (HALF-SIB)	7.1509	CRy=	-2.1574	4.2403	CRx=	-1.4527	
GENETIC CORRELATIONS	-0.3215	S.E.	0.2888				
PHENOTYPIC CORRELATIONS INDIVIDUAL	0.0096						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	-0.2975						
ENVIRONMENTAL CORRELATIONS	0.0669						

APPENDIX E: Tables of means and analyses of variance and covariance for wood density traits.

TABLE E1. Means and standard deviations for wood density at site CLES.

GROUP	COUNT	MEAN	STANDARD DEVIATION	STANDARD ERROR	MINIMUM	MAXIMUM	95 PCT CONF INT FOR MEAN	
SEED PARENTS								
110	99	339.4949	24.2558	2.4378	285.2000	404.0000	334.6572 TO	344.3327
408	103	345.6184	21.3852	2.1071	296.5000	440.9000	341.4389 TO	349.7980
193	105	345.8324	22.6667	2.2120	288.1000	410.1000	341.4458 TO	350.2189
623	94	347.7500	24.5873	2.5360	303.0000	418.2000	342.7140 TO	352.7860
314	101	351.6050	20.1674	2.0067	311.0000	401.6000	347.6236 TO	355.5863
549	102	352.6010	26.2154	2.5957	299.1000	405.1000	347.4518 TO	357.7502
418	99	357.1576	22.4651	2.2578	310.5000	412.4000	352.6770 TO	361.6382
300	97	357.4979	20.7526	2.1071	315.2000	409.7000	353.3154 TO	361.6805
310	100	357.8410	23.9978	2.3998	302.1000	442.8000	353.0793 TO	362.6027
439	96	363.2437	22.5989	2.3065	318.2000	419.5000	358.6648 TO	367.8227
422	98	364.0592	19.6184	1.9818	299.5000	423.9000	360.1259 TO	367.9924
72	96	364.6208	21.6802	2.2127	314.1000	419.6000	360.2280 TO	369.0136
73	102	368.1598	26.9444	2.6679	308.6000	429.9000	362.8674 TO	373.4522
57	99	368.5313	23.2008	2.3318	304.1000	417.2000	363.9040 TO	373.1586
303	95	370.3432	19.4941	2.0000	322.6000	413.8000	366.3720 TO	374.3143
49	95	370.5537	25.9850	2.6660	316.1000	432.8000	365.2603 TO	375.8471
315	102	371.5627	23.9418	2.3706	314.1000	431.1000	366.8601 TO	376.2654
60	102	375.6892	22.4611	2.2240	325.3000	441.6000	371.2774 TO	380.1010
415	99	377.4798	21.5213	2.1630	324.8000	431.2000	373.1875 TO	381.7721
323	97	377.4938	20.5047	2.0819	326.0000	434.7000	373.3612 TO	381.6264
499	98	379.0745	24.0179	2.4262	322.4000	439.3000	374.2592 TO	383.8898
305	94	382.8223	27.8421	2.8717	323.2000	445.6000	377.1197 TO	388.5249
POLLEN PARENTS								
448	544	354.9105	24.2572	1.0400	285.2000	442.8000	352.8675 TO	356.9534
24	540	363.9013	27.3602	1.1774	292.6000	445.6000	361.5885 TO	366.2141
33	539	364.1707	25.8854	1.1150	288.1000	440.9000	361.9805 TO	366.3609
62	550	369.0138	24.3616	1.0388	307.6000	434.7000	366.9733 TO	371.0543
TOTAL	2173	363.0113	25.9797	.5573	285.2000	445.6000	361.9184 TO	364.1043

TABLE E2. Analysis of variance for wood density (WD) at the Cowichan Lake site (CLES).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	56492.28	75.454	55.166		10.55%		
MALE	3	18752.98	31.113	21.903		4.35%		
FEMALE	21	15137.61	143.079	45.300	3.295	20.01%	14.913	0.000
R * M	6	1847.86	4.614	5.151		0.65%	1.849	0.095
R * F	42	1001.74	0.0	7.535		0.0 %	1.002	0.479
M * F	63	1012.69	0.0	8.819		0.0 %	1.013	0.466
R*M*F	126	999.34	75.318	15.404	2.391	10.53%	2.592	0.0
WITHIN	1909	385.52	385.523	12.472	5.409	53.91%		
ADDITIVE GENETIC VARIANCE			572.316	181.198	6.590			
DOMINANCE GENETIC VARIANCE			0.0	35.276	0.0			
TOTAL PHENOTYPIC VARIANCE			639.647		6.967			
PHENOTYPIC VARIANCE HALF-SIB			153.197		3.410			
PHENOTYPIC VARIANCE FULL-SIB			214.709					
HERITABILITY (INDIVIDUAL)			0.895	0.283		%RESPONSE/i =	6.234	
HERITABILITY (HALF-SIB)			0.934	0.296		%RESPONSE/i =	6.369	
HERITABILITY (FULL-SIB)			0.811	0.422				

TABLE E3. Means and standard deviations for Pilodyn values at site CLES.

GROUP	COUNT	MEAN	STANDARD DEVIATION	STANDARD ERROR	MINIMUM	MAXIMUM	95 PCT CONF INT FOR MEAN	
SEED PARENTS								
305	94	148.9787	17.7146	1.8271	108.0000	193.0000	145.3504 TO	152.6070
323	97	153.2887	15.5382	1.5777	118.0000	195.0000	150.1570 TO	156.4203
499	98	157.0204	17.9271	1.8109	115.0000	200.0000	153.4263 TO	160.6146
415	99	157.6162	15.4621	1.5540	130.0000	203.0000	154.5323 TO	160.7000
57	99	159.5758	19.2715	1.9369	120.0000	223.0000	155.7321 TO	163.4194
315	102	160.6765	17.3006	1.7130	120.0000	200.0000	157.2783 TO	164.0746
303	95	160.7368	16.1668	1.6587	130.0000	203.0000	157.4435 TO	164.0302
49	95	162.0947	19.8928	2.0410	108.0000	208.0000	158.0424 TO	166.1471
73	102	162.1471	20.8000	2.0595	113.0000	220.0000	158.0615 TO	166.2326
72	96	163.4375	17.1113	1.7464	123.0000	198.0000	159.9704 TO	166.9046
60	102	165.4314	16.5347	1.6372	125.0000	215.0000	162.1837 TO	168.6791
3[illegible]	101	168.1287	17.9998	1.7910	128.0000	218.0000	164.5753 TO	171.6821
4[illegible]	99	169.9394	21.1437	2.1250	128.0000	225.0000	165.7224 TO	174.1564
422	98	170.1429	19.2354	1.9431	130.0000	220.0000	166.2864 TO	173.9993
439	96	170.6875	17.2574	1.7613	135.0000	210.0000	167.1908 TO	174.1842
300	97	172.1753	19.4519	1.9750	128.0000	230.0000	168.2548 TO	176.0957
310	100	172.7700	18.4511	1.8451	125.0000	213.0000	169.1089 TO	176.4311
408	103	173.9903	17.5015	1.7245	135.0000	235.0000	170.5698 TO	177.4108
549	102	174.6176	18.4198	1.8238	140.0000	218.0000	170.9997 TO	178.2356
623	94	180.6489	17.3526	1.7898	133.0000	225.0000	177.0948 TO	184.2031
110	99	183.9192	23.8668	2.3987	140.0000	253.0000	179.1590 TO	188.6793
193	105	184.6095	20.0890	1.9605	135.0000	230.0000	180.7218 TO	188.4972
POLLEN PARENTS								
62	550	161.4218	18.3829	.7838	108.0000	215.0000	159.8821 TO	162.9615
33	539	164.7254	19.9710	.8602	108.0000	230.0000	163.0356 TO	166.4152
448	544	169.9890	18.8428	.8079	125.0000	225.0000	168.4020 TO	171.5759
24	540	172.0907	23.1865	.9978	118.0000	253.0000	170.1307 TO	174.0508
TOTAL	2173	167.0373	20.5968	.4418	108.0000	253.0000	166.1708 TO	167.9038

TABLE E4. Analysis of variance for Pilodyn measures (PIN) at the Cowichan Lake site (CLES).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	36459.51	48.889	35.604		10.76%		
MALE	3	12654.70	20.391	14.778		4.49%		
FEMALE	21	8871.27	81.637	26.566	5.409	17.97%	10.924	0.000
R * M	6	1198.61	3.411	3.335		0.75%	2.088	0.059
R * F	42	429.98	0.0	3.549		0.0 %	0.749	0.858
M * F	63	956.24	15.248	7.404		3.36%	1.666	0.008
R*M*F	126	574.11	40.467	8.859	3.808	8.91%	2.350	0.0
WITHIN	1909	244.32	244.320	7.904	9.358	53.77%		
ADDITIVE GENETIC VARIANCE			326.550	106.266	10.818			
DOMINANCE GENETIC VARIANCE			60.994	29.615	4.676			
TOTAL PHENOTYPIC VARIANCE			405.474		12.055			
PHENOTYPIC VARIANCE HALF-SIB			91.258		5.719			
PHENOTYPIC VARIANCE FULL-SIB			140.554					
HERITABILITY (INDIVIDUAL)			0.805	0.262		%RESPONSE/I =	9.709	
HERITABILITY (HALF-SIB)			0.895	0.291		%RESPONSE/I =	10.232	
HERITABILITY (FULL-SIB)			0.834	0.378				

TABLE E5. Analysis of variance for diameter at the Cowichan Lake site (CLES) (for the wood density measured trees).

SOURCE	D.F.	MEAN SQUARE	VAR.COMP.	S.E.	C.V.	VAR.COMP.%	F.RATIO	PROBABILITY
REP	2	5732.55	6.803	5.635		4.83%		
MALE	3	205.72	0.0	0.907		0.0 %		
FEMALE	21	1051.05	7.851	3.309	3.225	5.57%	3.745	0.007
R * M	6	934.84	2.955	2.597		2.10%	2.376	0.033
R * F	42	269.33	0.0	2.301		0.0 %	0.685	0.920
M * F	63	404.67	0.230	3.503		0.16%	1.029	0.439
R*M*F	126	393.38	37.811	6.043	7.076	26.84%	4.616	0.0
WITHIN	1909	85.23	85.234	2.757	10.624	60.50%		
ADDITIVE GENETIC VARIANCE			31.406	13.236	6.449			
DOMINANCE GENETIC VARIANCE			0.919	14.011	1.103			
TOTAL PHENOTYPIC VARIANCE			134.081		13.325			
PHENOTYPIC VARIANCE HALF-SIB			11.892		3.968			
PHENOTYPIC VARIANCE FULL-SIB			24.031					
HERITABILITY (INDIVIDUAL)			0.234	0.099		%RESPONSE/i =	3.121	
HERITABILITY (HALF-SIB)			0.660	0.278		%RESPONSE/i =	5.240	
HERITABILITY (FULL-SIB)			0.336	0.275				

TABLE E6. Components of variance and covariance for traits WD and DM12.

FOR VARIABLES	WD			DM12			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	143.0790	S.E.	45.2995	7.8514	S.E.	3.3091	-17.8360
ADDITIVE GENETIC VARIANCE	572.3159	S.E.	181.1981	31.4056	S.E.	13.2363	-71.3440
DOMINANCE GENETIC VARIANCE	0.0	S.E.	35.2759	0.9188	S.E.	14.0111	-0.4594
PHENOTYPIC VARIANCE INDIVIDUAL	639.6467			134.0806			-121.0718
PHENOTYPIC VARIANCE HALF-SIB	153.1971			11.8917			-20.9254
PHENOTYPIC VARIANCE FULL-SIB	214.7094			24.0306			-27.6289
HERITABILTY FOR INDIVIDUAL SELECTION	0.8947	S.E.	0.2833	0.2342	S.E.	0.0987	0.4578
COEFFICIENT OF VARIATION (PI)	6.9671			13.3252			
%RESPONSE /i (INDIVIDUAL)	6.2337			3.1211			
HERITABILTY FOR HALF-SIB SELECTION	0.9340	S.E.	1.1828	0.6602	S.E.	1.1131	0.7853
COEFFICIENT OF VARIATION (PHS)	3.4096			3.9684			
%RESPONSE /i (HALF-SIB)	3.1844	CRy=	-1.4248	2.6201	CRx=	-1.6583	
GENETIC CORRELATIONS	-0.5322	S.E.	0.1852				
PHENOTYPIC CORRELATIONS INDIVIDUAL	-0.4134						
PHENOTYPIC CORRELATIONS H S FAMILIES	-0.4903						
ENVIRONMENTAL CORRELATIONS	-0.5981						

TABLE E7. Components of variance and covariance for traits WD and PIN.

FOR VARIABLES	WD			PIN			COVARIANCE
FEMALE HALF-SIB FAMILY VARIANCE	143.0790	S.E.	45.2995	81.6374	S.E.	26.5664	-102.8783
ADDITIVE GENETIC VARIANCE	572.3159	S.E.	181.1981	326.5496	S.E.	106.2656	-411.5129
DOMINANCE GENETIC VARIANCE	0.0	S.E.	35.2759	60.9936	S.E.	29.6150	-25.7648
PHENOTYPIC VARIANCE INDIVIDUAL	639.6467			405.4741			-358.5381
PHENOTYPIC VARIANCE HALF-SIB	153.1971			91.2580			-110.9650
PHENOTYPIC VARIANCE FULL-SIB	214.7094			140.5540			-146.7549
HERITABILTY FOR INDIVIDUAL SELECTION	0.8947	S.E.	0.2833	0.8054	S.E.	0.2621	0.8489
COEFFICIENT OF VARIATION (PI)	6.9671			12.0550			
%RESPONSE /i (INDIVIDUAL)	6.2337			9.7086			
HERITABILTY FOR HALF-SIB SELECTION	0.9340	S.E.	1.1828	0.8946	S.E.	1.1645	0.9141
COEFFICIENT OF VARIATION (PHS)	3.4096			5.7190			
%RESPONSE /i (HALF-SIB)	3.1844	CRy=	-2.9667	5.1161	CRx=	-4.9761	
GENETIC CORRELATIONS	-0.9519	S.E.	0.0213				
PHENOTYPIC CORRELATIONS INDIVIDUAL	-0.7040						
PHENOTYPIC CORRELATIONS H.S. FAMILIES	-0.9385						
ENVIRONMENTAL CORRELATIONS	0.7267						